ESTIMATING ^{13}C AND ^{15}N TURNOVER RATES IN THE ARCTIC AMPHIPOD *ONISIMUS LITORALIS*: IMPLICATIONS FOR ANALYZING THE TRANSFER OF SEA ICE PRODUCTION TO UNDER-ICE FAUNA

By

Mette R. Nielson

RECOMMENDED:

Advisory Committee Chair

Head, Program in Marine Science and Limnology

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

November 21, 2006

Date

ESTIMATING ^{13}C AND ^{15}N TURNOVER RATES IN THE ARCTIC AMPHIPOD *ONISIMUS LITORALIS*: IMPLICATIONS FOR ANALYZING THE TRANSFER OF SEA ICE PRODUCTION TO UNDER-ICE FAUNA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Mette R. Nielson, B. S.

Fairbanks, Alaska

December 2006

Abstract

The Arctic amphipod *Onisimus litoralis* migrates from the seafloor to the sea ice to graze on ice algae, a rich food source during the Arctic spring, resulting in complex trophic dynamics. I assessed the effect of temperature and season on the rate of change in stable isotopic composition of amphipods by simulating a diet switch in the laboratory using amphipods collected near Barrow, Alaska in spring and autumn 2004. Additionally, the proportional contributions of food sources to the amphipods' diet in the field were estimated. Isotopic change occurred faster in spring with half-lives of 13.9 (1°C) and 18.7 (4°C) days for carbon and 22.4 days for nitrogen compared to autumn rates of 77 (carbon) and 115 days (nitrogen). Temperature did not have a significant effect on turnover. Change occurred primarily through metabolic turnover (versus growth-related dilution) and was responsible for 84-89% of the change in carbon and 67-77% of the change in nitrogen in both seasons. A two-source mixing model estimated that ice-derived biota contributed 59 (±17)% to the amphipods' diet in May. These data show that the rate of isotopic change can vary temporally for a single species, highlighting the importance of experimental work for interpreting stable isotope field-data.

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Acknowledgements

This research was supported by grants from Alaska Sea Grant and the Center for Global Change. I want to thank Dr. Susan Sugai for her special attention and interest in the successful completion of this project. I am grateful to the staff of the Barrow Arctic Science Consortium who greatly simplified field logistics, and I want to thank Sarah Story, Sang Lee, Klaus Meiners, and Max Kaufman for their assistance in Barrow. I would like to thank Tim Howe and Norma Haubenstock and the Alaska Stable Isotope Facility for analyzing the many stable isotope samples collected for this research. I also want to thank the School of Fisheries and Ocean Sciences and its office staff, with special thanks to Christina Neumann, for their support and assistance. I am very grateful to my advisory committee members, Dr. Bodil Bluhm, Dr. Michael Castellini, Dr. Diane O'Brien, and Dr. Mat Wooller for their very helpful suggestions and valuable contributions to this thesis. Finally, I need to thank my major advisor, Dr. Rolf Gradinger for his scientific contributions to this research, and also for his professionalism and his mentorship throughout my graduate program.

1. Introduction

Sea ice is a prominent feature of the Arctic Ocean covering between 6.2 x 10^6 km^2 in the summer and 13.9 x 10^6 km^2 in the winter (Wadhams 2000). Unlike freshwater ice, frozen seawater is permeated by a network of brine-filled channels that are created as salts are expelled during ice crystal growth. These channels create a unique habitat for a specialized community of organisms, including bacteria, proto- and metazoans, and ice algae (Horner et al. 1992, Gradinger 2002), that combined contribute on average 57% of the total primary production in the central Arctic and 3% in the surrounding regions (Gosselin et al. 1997). Pennate diatoms are the most conspicuous members of the ice algal assemblage, though various groups of autotrophic flagellates are important contributors to sea ice primary production. Both benthic and pelagic metazoan taxa inhabit the ice, including rotifers, nematodes, polychaete larvae, turbellarians, crustacean nauplii, and harpacticoid and cyclopoid copepods (Carey 1992, Schnack-Schiel 2003).

During early spring, when light penetration to the water column is low and phytoplankton production is limited, ice algal abundances can be orders of magnitude higher than phytoplankton abundance, providing an important early food source (Horner 1985, Sakshaug et al. 1994). The highest ice algal abundances occur in the bottom few centimeters where temperature and salinity fluctuations are moderated by the underlying seawater, and nutrient exchange is maximized (Horner 1985, Horner et al. 1992). Sympagic (ice-associated) fauna take advantage of this rich food source near the ice-water interface (Werner 1997, Poltermann 1998). The trophic transfer of ice-derived material to benthic consumers has been the focus of a few recent studies (Cooper et al. 2002, Ambrose et al. 2005, McMahon et al. 2006), but even fewer studies have quantified the direct transfer of ice biota to higher trophic levels through sympagic fauna (Werner 2000, Auel et al. 2002). Ice-derived organic carbon is channeled from sea ice biota through sympagic amphipods to fish, birds, and mammals (Bradstreet and Cross 1982, Lønne and Gabrielsen 1992, Tynan and DeMaster 1997). However it remains unknown

how important this ice-based food web is relative to the pelagic or benthic food webs throughout a full seasonal cycle for any location in the Arctic.

Over the past several decades both sea ice extent and duration have decreased (Rothrock et al. 1999, Johannessen et al. 2004) and are expected to lead to reduced ice algal production as warming continues (Lavoie et al. 2005). As sea ice patterns are altered, changes in important prey species abundances and distributions will ultimately affect higher trophic organisms including birds (Lønne and Gabrielsen 1992) and marine mammals (Tynan and DeMaster 1997). To help shed light on the role of sea ice production for higher trophic levels, this study focuses on sympagic amphipods, as they are a major connector between the sea ice, the water column, and the benthos (Werner 2000, Peinert et al. 2001).

Sympagic, autochthonous (permanently associated with the ice) gammaridean amphipods are the primary constituents of the sub-ice community under offshore Arctic pack ice (Lønne and Gulliksen 1991, Carey 1992, Werner and Gradinger 2002, Gradinger and Bluhm 2004). *Apherusa glacialis, Onisimus glacialis, O. nanseni*, and *Gammarus wilkitzkii* occur in this habitat during all seasons (Werner and Auel 2005). They can graze 1.1 to 2.6% d^{-1} of the ice algal standing stock (Werner 1997), and thereby make this production available to larger organisms including fish, birds, and seals (Bradstreet and Cross 1982). Near-shore pack and fast ice is colonized by benthic amphipods like *Onisimus litoralis* (Boudrias and Carey 1988) that migrate between the ice and the benthos (Carey 1992) and play a similar role in transferring ice-produced organic matter to larger organisms. Amphipods are a major prey item for Arctic cod (*Boreogadus saida*), making *O. litoralis* an important trophic link between ice biota and higher trophic levels in coastal Arctic waters (Bradstreet and Cross 1982, Hobson and Welch 1992).

Analysis of naturally occurring stable isotope ratios of carbon and nitrogen has become a standard method in both field and laboratory food web studies, as the isotopic

composition of a food source is reflected in the isotopic composition of the consumer in a fairly predictable manner (Hobson and Clark 1992, Bosely et al. 2002). The stable carbon isotope composition ($\delta^{13}C$) of a consumer is similar to that of its diet, generally enriched by 0 to 1‰, while a consumer's stable nitrogen isotope composition ($\delta^{15}N$) reflects a stepwise increase from diet to consumer of 2 to 4‰ (Peterson and Fry 1987). Both isotopes are useful as dietary tracers, integrating carbon and nitrogen sources over a period of time, as opposed to giving a snapshot of the most recent meal, as is the case in gut content analysis. In addition, the larger difference between $\delta^{15}N$ of a consumer and its diet can be used to estimate trophic position within a food web. This difference between the isotopic composition of a consumer and its diet (fractionation) occurs when isotopically lighter isotopes are preferentially excreted, leaving the consumer's tissues isotopically heavier (more enriched in the heavier isotope) than its diet (DeNiro and Epstein 1981, Peterson and Fry 1987).

In the ice-covered coastal waters of the Arctic, phytoplankton and ice algae, the two main primary producers, can have distinctly different isotopic signatures. A typical high latitude marine phytoplankton community has a $\delta^{13}C$ signature of –27 to –25‰ (Hobson and Welch 1992, Iken et al. 2005, Dunton et al. accepted). The limited diffusive supply of CO_2 into the network of brine channels within sea ice can cause CO_2 limitation to the ice algae, resulting in higher $\delta^{13}C$ values in ice algae relative to phytoplankton in the underlying water column (Gleitz et al. 1995, Thomas and Dieckmann 2003). Arctic sea ice algae can thereby reach $\delta^{13}C$ values of –20 to –10‰ (Hobson and Welch 1992, Gradinger and Bluhm 2005, McMahon et al. 2006, Tamelander et al. 2006). This difference between sea ice algae and phytoplankton offers an opportunity to use stable isotopes to determine the contribution of each carbon source to the diet of *O. litoralis*.

The interpretation of stable isotope compositions of animals can be complicated by a number of factors. In their natural environment animals may not be in isotopic equilibrium with their diet due to migratory movement or seasonal changes in available

food sources (Hobson 1999, Schmidt et al. 2003). When an animal changes its diet from one isotopically distinct food source to another, the stable isotope value of the new diet is not immediately reflected in the tissues of the consumer (Tieszen et al. 1983, Hobson and Clark 1992, Post 2002). The time required for a consumer's tissue to reach isotopic equilibrium after a diet switch varies with taxon, life stage, the tissue being analyzed, and the environment (Fry and Arnold 1982, Hobson and Clark 1992, Frazer et al. 1997). Following a change in diet, stable isotopic change in organisms occurs through two processes. First, new tissue synthesized after the diet switch will reflect the isotopic composition of the new diet, and the rate of growth will directly affect the rate of isotopic change (Fry and Arnold 1982). Secondly, metabolic turnover of tissues synthesized from the previous diet will result in a shift in isotopic composition towards that of the new diet (Hobson and Clark 1992).

Knowledge about the time required for a consumer to equilibrate with the isotopic composition of its current diet is essential in order to interpret stable isotope values for trophic interactions (Gannes et al. 1997, Bosley et al. 2002), yet isotopic turnover has been determined for few animals, and to our knowledge, there are no published turnover rates for any Arctic marine organisms. In sea ice covered regions, temporal changes in the ice algal isotopic baseline can confound interpretation of stable isotope data if recent changes in the isotopic baseline have not yet been expressed in the tissues of consumers. Moreover, diet switching is likely in the Arctic, where strong seasonal pulses of production can lead to seasonally available food sources that are exploited by consumers during the short productive season (Legendre et al. 1992, Dower et al. 1996).

Isotopic change in rapidly growing ectotherms is primarily driven by growth (Fry and Arnold 1982, Herzka and Holt 2000, Bosley et al. 2002), while metabolic requirements have been shown to drive isotopic change in adult, non-growing endotherms (Tieszen et al. 1983, Hobson and Clark 1992, MacAvoy et al. 2005). In polar regions, slow growth among ectotherms is common (Brey et al. 1995, Bluhm et al. 1998, Peck 2002).

However, few studies have focused on slow-growing ectotherms to determine how metabolic turnover contributes to isotopic change. The majority of these studies have focused on temperate fish species (Hesslein et al. 1993, MacAvoy et al. 2001, Tominaga et al. 2003, Jardine et al. 2004, Sakano et al. 2005). Frazer et al. (1997) provided the first and so far only data for a polar invertebrate and found that metabolic turnover can be important in Antarctic larval krill *Euphausia superba*. Published results for aquatic ectotherms representing various taxa, stages of development, and environmental temperatures show a broad range of isotopic turnover rates (Fry and Arnold 1982, Bosley et al. 2002, Sakano et al. 2005, Jardine et al. 2006, McIntyre and Flecker 2006). These results highlight the need for experimentally determined turnover rates on species of interest in a particular environmental setting to more accurately interpret trophic dynamics and interactions in food web studies.

Here, stable isotopic changes following a diet switch were monitored in the gammaridean amphipod *O. litoralis* to provide the first isotopic turnover data for an Arctic marine invertebrate. Additionally, an experiment was carried out to investigate the effect of fasting on the stable isotope composition of *O. litoralis*. These data provide the foundation for using stable isotope ratios to examine the temporal dynamics of stable isotopic composition in ice-associated fauna that exhibit habitat or dietary changes as a response to seasonally available sea ice in coastal Arctic waters. The objectives of the field study were to i) collect *O. litoralis* and its potential food sources in the field to track trophic changes throughout a complete ice cycle and ii) to apply mixing models to determine the relative contribution of ice-derived material to the nutrition of *O. litoralis* during periods of ice cover. The objectives of the laboratory experiments were to i) estimate isotopic turnover rates for *O. litoralis* through controlled diet switch experiments, ii) examine the effect of temperature and season on turnover rates, and iii) determine the effect of fasting on the isotopic composition of *O. litoralis* over time. These experiments provide calibration information essential for interpretation of *in situ*

field results and are compared to previous vertebrate and invertebrate stable isotope turnover studies.

2. Materials and methods

2.1 Field collections

Specimens of *O. litoralis* were collected in baited minnow traps under shore-fast sea ice in the Chukchi Sea near Barrow, Alaska (71.3359° N, -156.7070° W, Fig. 2.1) in March, May, and December 2004. The traps were deployed through holes in the ice 200 to 400 m offshore at a water depth of approximately 7 m. The baited traps were positioned within 1 m of the ice bottom and remained in the water for 24 to 48 hours during each deployment. Bait, consisting of canned cat food, artificial trout bait and salmon eggs, was wrapped in filter paper and screen material to prevent ingestion. In ice-free conditions in September 2004, traps were deployed attached to buoys at this location, but no specimens were collected. Instead, at this time *O. litoralis* were collected in nearby Elson Lagoon (71.3321° N, -156.5415° W) in traps 300 m offshore at 5 m water depth. Traps were positioned 2 m above the seafloor, attached to anchors at the seafloor and to buoys at the surface.

In March, May, and December, ten amphipods were immediately preserved in buffered 4% formaldehyde-seawater solution for gut content analysis (see 2.14). Ten additional amphipods were transferred to containers with clean seawater for 24 hours to clear their guts before being frozen for stable isotope analysis (see 2.13). In March and September the remaining animals were transported to a University of Alaska, Fairbanks (UAF) laboratory for long term (9 and 10 week) feeding experiments. Upon arrival in Fairbanks, the amphipods were placed in incubation chambers (Precision 815 and 818) in the dark at 1°C to acclimate for 1 week. No food was offered during this period.

Potential food sources were sampled at the time of each amphipod collection. For this purpose, four replicate samples of sea ice (except September), seawater, and seafloor surface sediment were collected and analyzed for chlorophyll *a* (chl *a*), phaeopigment (phaeo), particulate organic carbon (POC) and nitrogen (PON) concentrations, and $\delta^{13}C$

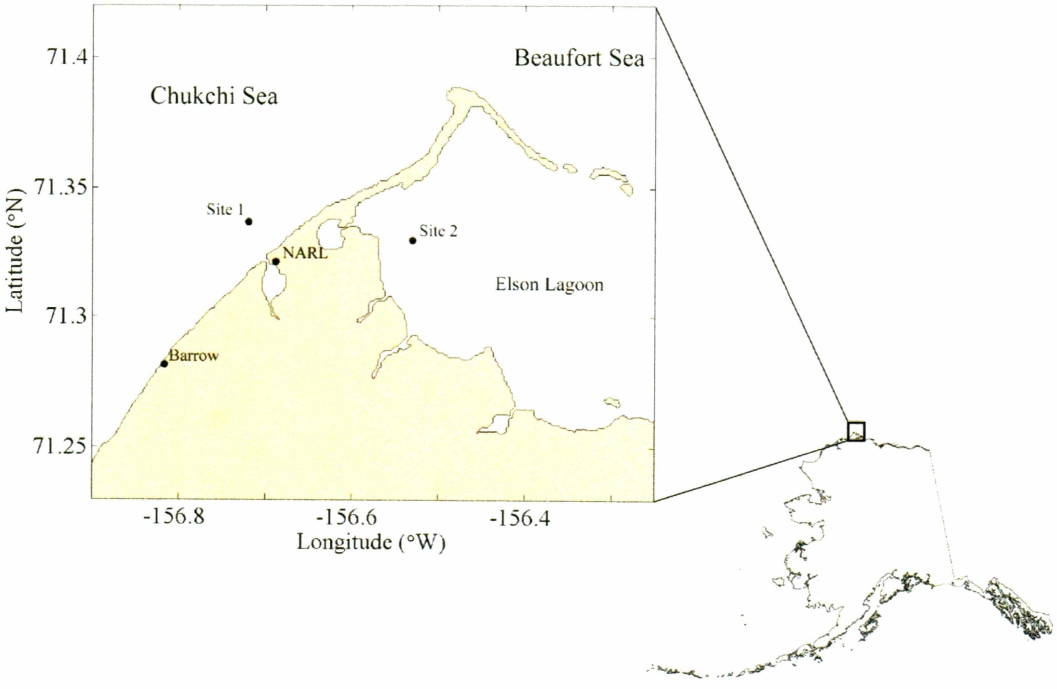

Fig. 2.1 Field study area near Barrow, AK. NARL = Navel Arctic Research Lab. Site 1 is the collection site for ice-covered periods (March, May and December 2004), Site 2 is the collection site for ice-free period (September 2004).

and $\delta^{15}N$ of the particulate organic matter (POM). Ice cores were collected with a Kovacs ice corer and bottom sections (10 cm) were melted in the dark in 800 ml of GF/F filtered seawater to reduce osmotic stress (Garrison and Buck 1986). Seawater was collected from 3 m water depth using a Kemmerer water sampler. Seawater and melted ice samples were filtered onto precombusted GF/F (0.7 μm) filters (25 mm). The top 2 cm of seafloor sediment were collected using a benthic corer deployed through ice core holes or from a boat during ice-free conditions. All samples were stored frozen at -18°C until analysis.

Ambient seawater temperature and salinity and ice temperature were measured during each sampling period. Seawater temperature and salinity were measured with a YSI 85 sensor underneath the ice (or from the water surface in September) at 1 m intervals. Ice temperature was measured with a Traceable thermometer along a complete core length at 10 cm intervals. Ice thickness was measured on a single ice core and snow depth was determined as the mean of ten measurements.

2.1.1 *Chlorophyll a analysis*

Chl *a* filters from water and melted ice samples were extracted in glass tubes with 7 ml 90% acetone and placed in a freezer (-18°C). After 24 hours the tubes were allowed to adjust to room temperature in the dark before being analyzed with a Turner TD700 fluorometer (Arar and Collins 1992).

Seafloor sediment samples were defrosted, and approximately 1 g of sediment was transferred to preweighed 25 ml glass vials. 15 ml 90% acetone was added to the vials that were then placed in the freezer at -18°C (Conde et al. 1999). After 24 hours the sediment in the vials was mixed thoroughly, and the liquid was decanted into 50 ml centrifuge tubes and centrifuged for 7 minutes at 4000 rpm. The supernatant was poured into glass tubes and allowed to come to room temperature prior to analysis. Chl *a* was

measured as above. The remaining sediment was then dried and weighed. Chl *a* concentration was standardized to sediment dry weight (see above).

2.1.2 *Proportional contribution of food sources*

Two- and three-source mixing models (Isoerror 1.04; http://www.epa.gov/wed/pages/models/isotopes/isoerror1_04.htm) were used to determine the relative contributions of particulate organic matter from sea ice (POM_{ice}), seawater (POM_{water}), and seafloor sediment (POM_{sed}) to field amphipod diets. The Isoerror program provides estimates (and 95% confidence intervals) of the proportional contribution of multiple diet sources to a consumer using linear mixing models (Phillips and Gregg 2003). Fractionation factors used in the mixing models (1‰ for $\delta^{13}C$ and 2.5‰ for $\delta^{15}N$) were chosen based on average values of published, experimentally determined fractionation factors for an amphipod (*Gammarus lawrencianus*) and isopod (*Idotea baltica*, McCutchan et al. 2003), and ghost shrimps (*Nihonotrypaea japonica* and *N. harmandi*, Yokoyama et al. 2005) because isotopic fractionation has not been experimentally assessed in *O. litoralis*.

2.1.3 *Stable isotope and POC/PON analysis*

Filters, amphipods, and experimental diet samples (see below) were oven dried for 24 hours at 60°C, fumed with HCl to remove carbonates, and re-dried for 48 hours at 60°C. Filters were packed directly into tin capsules. Feed samples and whole amphipods were homogenized using a mortar and pestle before being weighed into tin capsules. $\delta^{13}C$ and $\delta^{15}N$ were measured by continuous flow isotope ratio mass spectrometry, using a Costech elemental analyzer interfaced with a Thermo Finnigan Delta Plus Isotope Radio Mass-Spectrometer at the UAF Alaska Stable Isotope Facility. Isotope ratios were reported in per mil (‰) using the standard notation:

$$\delta X = \{(R_{sample}-R_{std})/R_{std}\} \times 1000\ (‰)$$

where X = ^{13}C or ^{15}N, R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and std (standard) = V-PDB (Vienna-Pee Dee Belemnite) or air N_2, respectively. Analytical precision was 0.1‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{15}N$ and was established by analyzing numerous (n=5-9) standards (peptone) throughout each run. The % carbon and % nitrogen were analyzed concurrently with isotope analysis.

2.1.4 *Gut content analysis*

Guts and stomachs of 30 amphipods, ten from each sampling period (except September), were extracted under a dissecting microscope and mounted in deionized water on glass slides. These were examined using a Zeiss inverted compound microscope at 300x magnification. Guts and stomachs were individually assigned arbitrary scores from 1 to 4 describing fullness (1: less than 25% full; 2: >25-50% full; 3: >50-75% full; 4: more than 75% of the volume filled). Items present in the digestive tract were categorized as algal cells, crustacean parts, detritus, and sediment grains; other categories could not be identified.

2.2 Turnover experiments

Two long term feeding experiments (63 and 72 days for experiments 1 (Exp 1) and 2 (Exp 2), respectively) were performed to estimate C and N turnover rates in amphipods collected during ice-covered (March) and ice-free (September) periods (see below). Exp 1 assessed the turnover of C and N at two different temperatures and for two different diets, while Exp 2 was conducted to compare the turnover in amphipods collected during an ice-free period to those collected during an ice-covered period.

Prior to the start of each feeding experiment, amphipods were blotted dry, weighed to the nearest 0.1 mg, digitally photographed for subsequent length measurements, and transferred to 500 ml plastic cups filled with artificial seawater (Instant Ocean ©, 30‰) at 1°C or 4°C in the dark. Each cup contained two animals, one serving as a backup in case the primary specimen died prior to sampling, separated by a screen to prevent

cannibalism. Length measurements, from the base of the antennae to the tip of the telson, were conducted using ImageJ image processing and analysis software (http://rsb.info.nih.gov/ij/).

2.2.1 *Experimental diets*

Three isotopically distinct experimental feeds were created using a combination of commercial algal-based aquaria fish food (Wardley® Premium Algae Discs™) and ice algae collected from the study site in June 2003. Ice algal cells were cultured in artificial seawater (Instant Ocean, 30‰), at 4°C under 24 hours of artificial light and constant aeration. Fresh artificial seawater and Guillard's f/2 (Sigma G9903) nutrient solution were added to the main culture weekly. Stable isotopic enrichment of the ice algae was accomplished through incorporation of heavy isotopes during algal incubations with ^{15}N and ^{13}C labeled compounds ($Na^{15}NO_3$ and $NaH^{13}CO_3$, respectively). Each week 2 L of the culture was transferred to a separate container and 0.8 ml labeled $Na^{15}NO_3$ solution (0.086 g/L) and 4 ml labeled $NaH^{13}CO_3$ solution (4.3 g/L) were added. Algal cells in the 2 L culture were incubated under the same environmental conditions as the main culture for 24 hours. After 24 hours, the enriched culture was centrifuged, the water was decanted, and algal cells were frozen. The isotopic signature incorporated by the algal cells was checked periodically during this period.

All isotopically enriched algal samples were pooled ($\delta^{13}C$ = 605.8 ‰, $\delta^{15}N$ = 44.0‰), dried for 3 days at 60°C, and ground using a Wig-L-Bug homogenizer. The commercial fish food ($\delta^{13}C$ = -22.8 (±0.4) ‰, $\delta^{15}N$ = 2.0 (±0.2) ‰, n=5) was homogenized in a food mill. Experimental diets were formulated by mixing different ratios of the isotopically enriched algae with the commercial food (Table 2.1). Deionized water was added to make a paste, and pellets of 2 mm diameter were portioned onto aluminum foil using a syringe. The pellets were dried at 60°C for 48 hours and stored at -18°C.

Table 2.1 Experimental temperatures and diets for turnover experiments. Diet $\delta^{13}C$ and $\delta^{15}N$ values are mean±SD (n=5). Experiment 1 (Exp 1) was run from April to June, and experiment 2 (Exp 2) was run from October to December, 2004.

Exp.	Treatment	T (°C)	Diet	Diet $\delta^{13}C$ (‰)	Diet $\delta^{15}N$
1	High $\delta^{13}C$ enrichment	1, 4	1	20.6±1.0	3.7±0.6
1	Moderate $\delta^{13}C$ enrichment	1	2	-15.4±0.6	2.5±0.6
1	Fasting	1	None	–	–
1	Control	1	3	-22.8±0.2	2.0±0.2
2	High $\delta^{13}C$ enrichment	1	1a	49.3±0.8	22.8±1.0
2	Control	1	3	-22.8±0.2	2.0±0.2

Pellets were soaked in artificial seawater to determine the stability of the isotopic values under experimental conditions. After soaking for 72 hours (the average time a food pellet would sit in an experimental cup before being replaced with a fresh pellet), pellets were re-dried and $\delta^{13}C$ and $\delta^{15}N$ values of the soaked pellets were measured. Soaking reduced the enrichment level of the enriched diets by approximately 10‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$. Diet values reported below are for soaked pellets. Soaking had no effect on the non-enriched diet.

The final isotope values for the experimental diets (Table 2.1) ranged from -22.8 (±0.2) to 49.3 (±0.8) ‰ for $\delta^{13}C$ and 2.0 (±0.2) to 22.8 (±1.0) ‰ for $\delta^{15}N$. The highly enriched diet, reformulated for the second experiment using algae enriched during a second set of incubations (pooled enriched ice algal values; $\delta^{13}C$=425.0‰, $\delta^{15}N$=112.4‰), is designated diet 1a. For both experiments a non-enriched diet, composed of non-enriched ice algae and the commercial food, served as a control.

2.2.2 *Experimental setup*

Exp 1 took place from April 2 to June 3, 2004, using amphipods collected in March 2004. Amphipods were randomly assigned to one of four treatments as outlined in Table 2.1. Each treatment consisted of five replicate animals and their backups for each of the ten sampling periods. Two treatments received the highly enriched diet (diet 1), one maintained at 1°C and the other at 4°C, to investigate the effect of temperature on carbon and nitrogen turnover. All other treatments were maintained at 1°C. The third treatment received the moderately enriched diet (diet 2) with a $\delta^{13}C$ value similar to values found in Barrow fast ice communities in late spring under bloom conditions (Gradinger et al. in review). The fourth treatment received no food but otherwise experienced the same conditions as the treatments above. A fifth group of amphipods received the non-enriched diet (diet 3) to serve as a control for weeks 1 through 3. At week 4, the control accidentally began receiving diet 1 for the duration of the experiment, leaving no control group from week 4 through the end of the experiment.

Amphipods were kept in the dark and fresh feed pellets were added every 3 days, at which time uneaten food and fecal pellets were suctioned off the bottom of the cups, and molts were collected. A third of the water volume in each cup was removed each week during cleaning and replaced with fresh artificial seawater. Incubation temperature was surveyed daily and dead animals were removed.

Initial amphipod $\delta^{13}C$ and $\delta^{15}N$ ratios determined at the start of the experiment. Thereafter, 5 replicate amphipods (and their backups) were sampled weekly from each treatment. Sampled amphipods were transferred to cups containing clean artificial seawater and allowed to clear their guts for 24 hours. They were then blotted dry, weighed to the nearest 0.1 mg wet weight (WW), photographed to determine length, and frozen at -18°C until processed for stable isotopic analysis.

Exp 2 took place from October 1 to December 25, 2004. The low number of amphipods collected in September and that survived the transfer to the Fairbanks laboratory allowed for only two treatments: one receiving the highly enriched diet (diet 1a) and the other receiving the non-enriched diet as control. Both groups were maintained in the dark at 1°C. During Exp 1 much of the isotopic turnover occurred in the first three weeks. Therefore, amphipods were sampled every four days in the first two weeks of Exp 2. Sampling was then extended to every seven days at week 3, and finally every ten days from week 6 to the end of the experiment. Upon sampling, amphipods were processed as described for Exp 1.

2.2.3 *Turnover rate modeling*

Turnover rates were calculated as a function of days since the diet switch using the equation (Tieszen et al. 1983):

Eq. (1) $$\delta_{(t)} = \delta_f + (\delta_0 - \delta_f)\, e^{-c\,t}$$

where $\delta_{(t)} = \delta^{13}C$ or $\delta^{15}N$ (‰) at time t, δ_f = the value (‰) being approached asymptotically, δ_0 = the amphipod $\delta^{13}C$ or $\delta^{15}N$ in equilibrium with the old diet (‰), c = the fractional turnover rate constant (d^{-1}) and t = time (d) since diet switch. $\delta_{(t)}$, δ_0, and t were known. The model was used to estimate the parameters c and δ_f.

Isotopic change rate is often expressed as a half-life. Half-life refers to the amount of time required for the stable isotope signature of the consumer's tissues to reach a midpoint value between the equilibrium value of the consumer before the diet switch and the expected equilibrium value of the consumer on the new diet (Bosley et al. 2002). Half-life was calculated as $HL = \ln(0.5) / c$.

Fractional turnover rates obtained using this model provide estimates of the time required for the tissues of *O. litoralis* to reflect a switch to an isotopically distinct diet. However, the model does not provide information about the relative contribution of metabolic turnover to isotopic change. To better understand the processes governing isotopic turnover in *O. litoralis*, we used a model that partitions the fractional turnover rate, c, into two components: growth (g = the growth rate in d^{-1}) and metabolic turnover (m = the metabolic turnover rate in d^{-1}) according to Hesslein et al. (1993):

Eq. (2) $$\delta_{(t)} = \delta_f + (\delta_0 - \delta_f)\, e^{-(g+m)\,t}$$

The growth rate was calculated as $g = \ln(W_f/W_0)/t$, where W_f is the amphipod (mg wet weight) at time of sampling and W_0 is the initial amphipod weight at the start of the experiment. The sum of (g+m) corresponds to the fractional turnover rate constant, c, and describes total isotopic change resulting from both growth (g) and metabolic turnover (m). Final equilibrium values (δ_f) estimated using Eq. 1 were used in Eq. 2.

2.2.4 *Statistical analysis*

All statistical analyses were performed in SYSTAT version 6.0 (SPSS Inc., Evenston, IL). The estimates of the fractional turnover rate constant (c) and the metabolic turnover rate (m) were obtained using nonlinear, iterative, least squares minimization techniques. Differences in isotopic turnover between temperature treatments was tested using a likelihood ratio test (Haddon 2001) that compares the total sum of squared residuals (RSS) for the two data sets pooled and fit with a single model to the sum of the RSS from fitting each data set with separate models. The resulting statistic is compared to a chi square distribution with the degrees of freedom equal to the number of constraints placed upon the fit (= estimated parameters).

3. Results

3.1 Field observations

3.1.1 *Environmental data*

Snow depth was similar in March, May, and December 2004, with means of 6.3 (±0.9), 6.5 (±0.4), and 7.8 (±1.2) cm, respectively (Table 3.1). Ice thickness in March was 143 cm and ice temperature ranged from -19.6°C at the surface to -2.0°C at the ice-water interface (Fig. 3.1). Ice thickness had increased by May to 175 cm, and the ice surface had warmed. A light sediment layer was observed 1 m from the surface at that time. In December, the newly forming sea ice was 56 cm thick at the time of sampling. Seawater temperatures in March and May ranged from -0.6°C at the seafloor to -1.7°C just below the ice. Seawater temperature was constant in December. Salinity ranged from 30.7‰ at the seafloor to 29.7‰ directly below the ice in March and May, and from 26.6 to 25.1‰ in December. In September the water temperature in Elson Lagoon was approximately 9°C with a salinity of 28.7‰.

3.1.2 *Chlorophyll a and POC*

From March to May, chl *a* concentration in the ice increased from 2.6 (±0.0) µg/L to 19.1 (±5.6) µg/L (Fig. 3.2a). Although the water chl *a* concentrations also increased (0.0 (±0.0) to 0.2 (±0.0) µg/L), they were about two orders of magnitude lower than those found in the ice. Pelagic chl *a* concentrations were highest for the season in August (0.5 (±0.0) µg/L). Phaeo concentrations were highest in May in both the ice and water column, with 1.7 (±0.8) and 0.2 (±0.1) µg/L, respectively. In December chl *a* concentrations were less than 0.1 (±0.0) µg/L in both the water column and in the newly formed sea ice. Seafloor sediment chl *a* and phaeo concentrations were highly variable. The highest and most variable values were found in March (0.6 (±0.3) µg/g dry weight (DW) chl *a* and 1.9 (±1.9) µg/g DW phaeo). Concentrations decreased in May to 0.3

Table 3.1 Field environmental measurements near Barrow, AK, 2004. Sea ice thickness and seawater temperature and salinity profile ranges are reported from directly below the ice (number on left in each column) to the seafloor (number on right within each column). In September, only a single temperature reading was taken, and the temperature profile was constant in December.

Month	Ice thickness (cm)	Snow depth (cm) ± SD	Seawater temperature (profile range) (°C)	Salinity (‰) (profile range)
March	143	6.3 ±0.9	-1.7 to -0.6	29.8 to 30.7
May	175	7.8 ±1.2	-1.7 to -1.5	29.7 to 30.4
August	—	—	5.9 to 6.0	24.6 to 24.8
September (Elson Lagoon)	—	—	9.0	—
December	56	6.5 ±0.4	-1.8	25.1 to 26.6

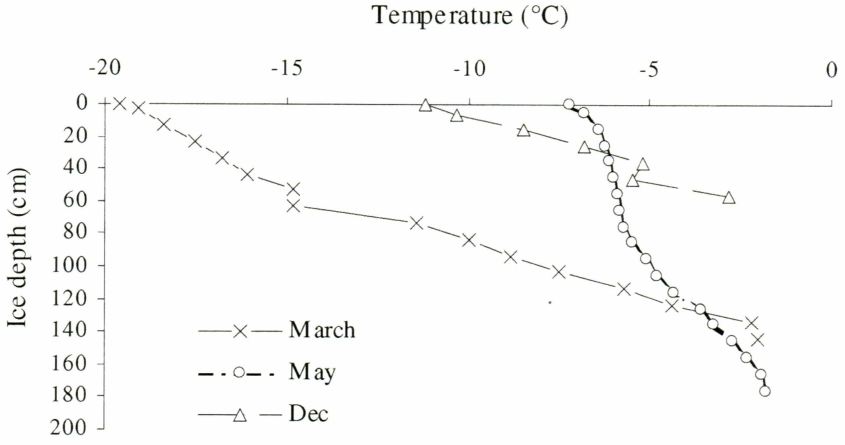

Fig. 3.1 Sea ice temperature profiles in land fast ice near Barrow Alaska, in March, May, and December 2004.

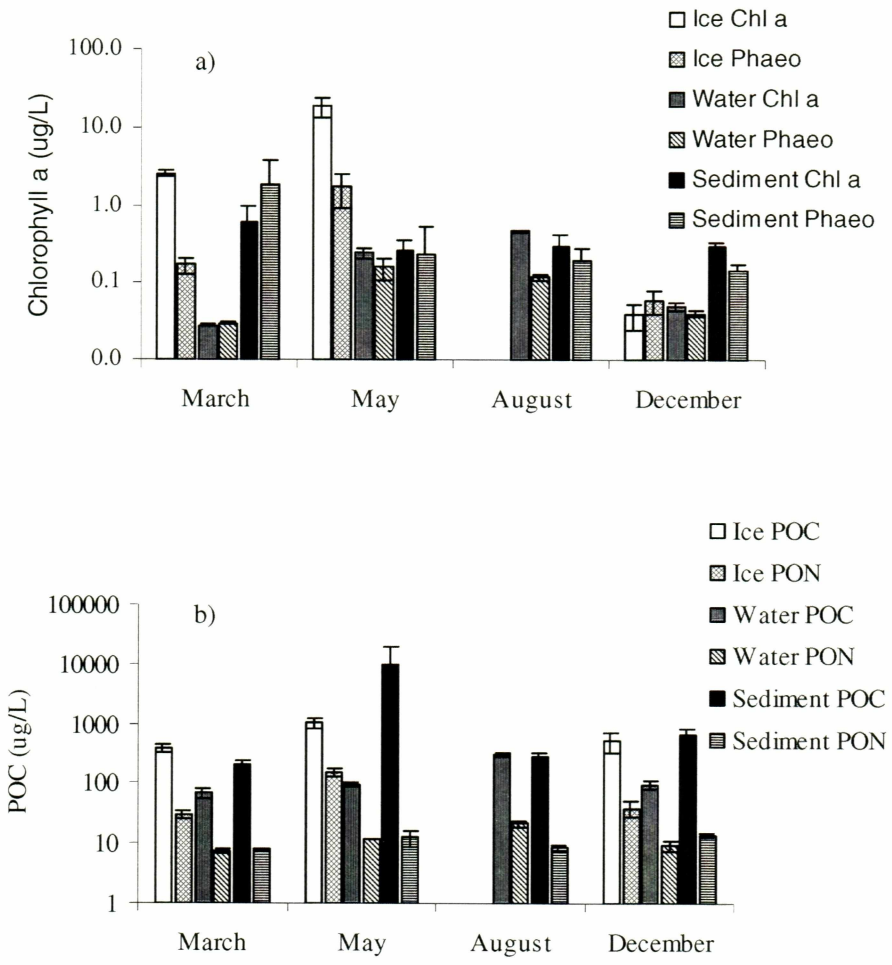

Fig. 3.2 Algal pigment and POC/PON concentrations in sea ice, water column, and seafloor sediments. All samples collected near Barrow, Alaska in 2004. a) Chlorophyll *a* (Chl *a*) and phaeophytin (Phaeo) and b) particulate organic carbon (POC) and nitrogen (PON). All values n=4. Error bars are SD.

(±0.1) and 0.2 (±0.3) µg/g DW for chl *a* and phaeo, respectively, and remained constant through the rest of the sampling periods.

POC_{ice} values were highest in May with 1031.0 (±63.7) µg/L (Fig. 3.2b), while the highest POC_{water} values occurred in August. POC_{sed} values ranged from 0.0 (±0.0) in March to 0.3 (±0.2) µg/g in May. In May, two of the four POM_{sed} replicates were more than an order of magnitude higher than all other samples throughout the season.

3.1.3 *Field isotope values and proportional contributions of food sources*

Mean POM_{ice} ranged from –24.0 (±0.3) to –23.2 (±0.4) ‰ for $\delta^{13}C$ and from 9.1 (±0.6) to 15.0 (±3.2) ‰ for $\delta^{15}N$ (Fig. 3.3). Mean POM_{water} ranged from –24.8 (±0.5) to –22.0 (±0.4) ‰ for $\delta^{13}C$ and from 10.6 (±1.0) to 16.6 (±0.7) ‰ for $\delta^{15}N$. POM_{ice} $\delta^{13}C$ and $\delta^{15}N$ changed little from March to May, while POM_{water} $\delta^{13}C$ showed a mean 1.5‰ enrichment during this period. POM_{sed} values were consistently lower in $\delta^{15}N$ (>13 ‰) relative to amphipod values and means ranged from -0.0 (±0.6) to 1.6 (±1.9) ‰. Mean POM_{sed} $\delta^{13}C$ ranged from –25.7 (±0.3) to –23.8 (±0.6) ‰. The $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios of amphipods collected in the coastal Chukchi Sea (March, May, and December) showed no change with season, with a maximum difference of 0.5‰ for $\delta^{13}C$ values and 0.4‰ for $\delta^{15}N$ values. The mean $\delta^{13}C$ and $\delta^{15}N$ ratios of amphipods collected in Elson Lagoon in September were enriched (–19.6 (±0.6) ‰ for $\delta^{13}C$, and 15.4 (±0.3) ‰ for $\delta^{15}N$) compared to those in the Chukchi Sea during all other sampling periods (–21.7 (±0.5) to –21.2 (±0.6) ‰ for $\delta^{13}C$ and 13.6 (±0.7) to 13.9 (±0.5) ‰ for $\delta^{15}N$). Therefore, inferences into their diet were not made using end members collected from the Chukchi Sea in August. (Note: amphipod $\delta^{13}C$ and $\delta^{15}N$ values plotted in Fig. 3.3 are corrected for fractionation; see 2.12).

The three-source mixing model was not able to estimate the contributions from the three potential end members using fractionation factors of 1‰ for $\delta^{13}C$ and 2.5‰ for $\delta^{15}N$. POM_{sed} $\delta^{15}N$ were 13-15‰ lower than *O. litoralis* $\delta^{15}N$ throughout the year, a difference

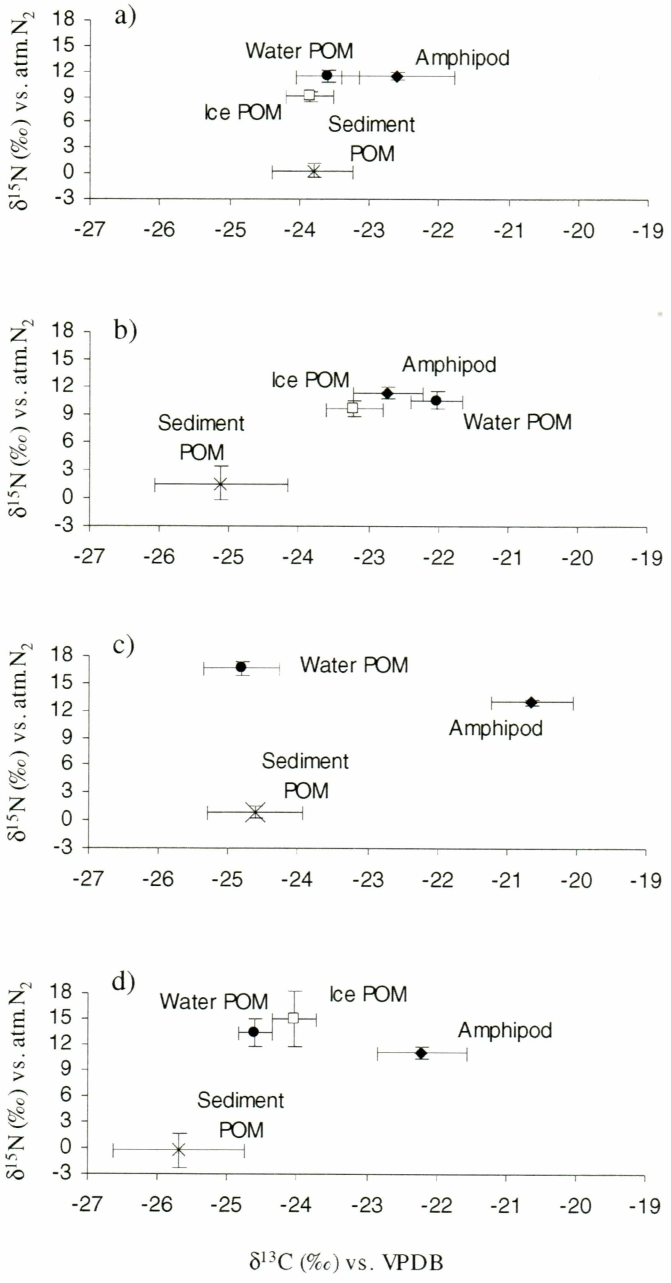

Fig. 3.3 Field $\delta^{13}C$ and $\delta^{15}N$ values for amphipods and potential diet items; sea ice, water column, and seafloor sediment POM in a) March, b) May, c) August, and d) December (n=10 for amphipod values, n=4 for POM values per sampling period), 2004. Amphipod values corrected for fractionation using 1.0‰ $\delta^{13}C$ and 2.5‰ $\delta^{15}N$. Values are expressed relative to the following standards: atmospheric nitrogen (atm. N_2) and Vienna-Pee Dee Belemnite (VPDB). Error bars are SD.

representing approximately four trophic levels, suggesting that POM_{sed} was not an important diet source. Therefore, a two-source mixing model was used to estimate relative contributions of POM_{ice} and POM_{water}. Using $\delta^{13}C$ ratios from May, this model estimated that *O. litoralis* was getting 59.2 (±17.8) % of its carbon from the ice and 40.8 (±17.8) % from the water column. POM_{ice} and POM_{water} isotope ratios were too similar in March and December to differentiate between the two sources.

3.1.4 *Gut content analysis*

Amphipod stomachs and guts were on average less then 25% full in March (Fig. 3.4a) with three amphipods having completely empty guts and/or stomachs. Stomachs and guts were on average nearly completely full in May and were 50 to 75% full in December. During all sampling periods amphipod guts contained primarily unidentifiable detritus, with only a few crustacean parts and sediment grains present (Fig. 3.4b). Algal cells (diatom frustules) were present in the gut of one amphipod sampled in May.

3.2 Experimental data

3.2.1*Growth and mortality*

O. litoralis collected in March were successfully transported from Barrow to the laboratory at UAF (travel time 2 hours) with <3% mortality, while the amphipods collected in September experienced >80% mortality during transport (travel time 2.5 hours) and acclimation to laboratory conditions. Amphipods in Exp 1 ranged in length from 1.1 to 1.7 cm and from 1.1 to 1.9 cm in Exp 2 (Fig. 3.5). Mean initial amphipod wet weight (WW) was 53.9 (±11.6) mg WW (n=250, Exp 1) in May and 55.3 (±28.1) mg WW (n=100, Exp 2) in September and increased over time in all fed treatments (Table 3.2). The weight range of amphipods included in Exp 2 was large, from 9.1 to 110.2 mg WW, due to the low number of surviving amphipods of a similar size that were collected

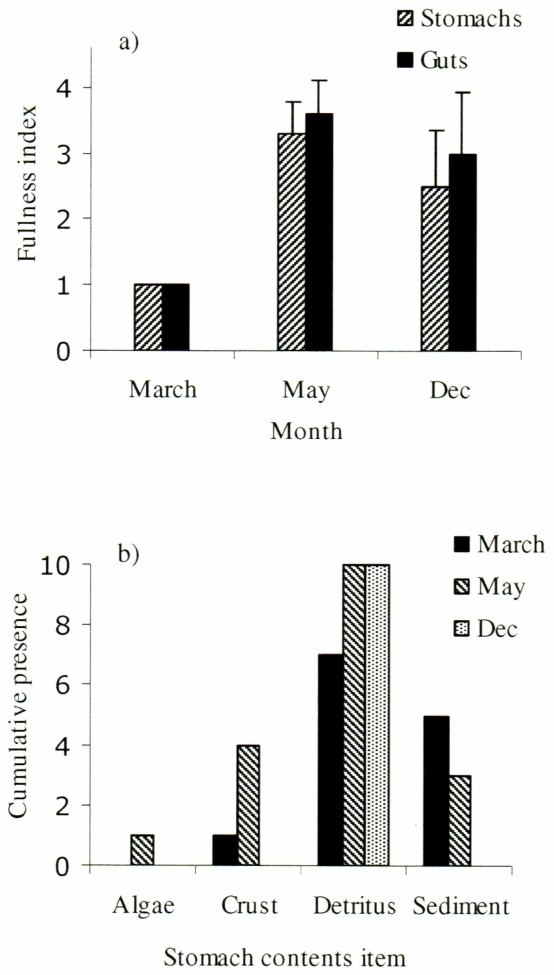

Fig. 3.4 *O. litoralis* gut contents in March, May, and December 2004. a) stomach and gut fullness and b) cumulative presence = number of amphipods out of ten per sampling period with the following identifiable items present in guts or stomachs: algae (algal cells/diatom frustules), crustacean parts (crust), detritus, and sediment grains. For explanation of stomach/gut fullness index see text. Error bars are SD, n=10.

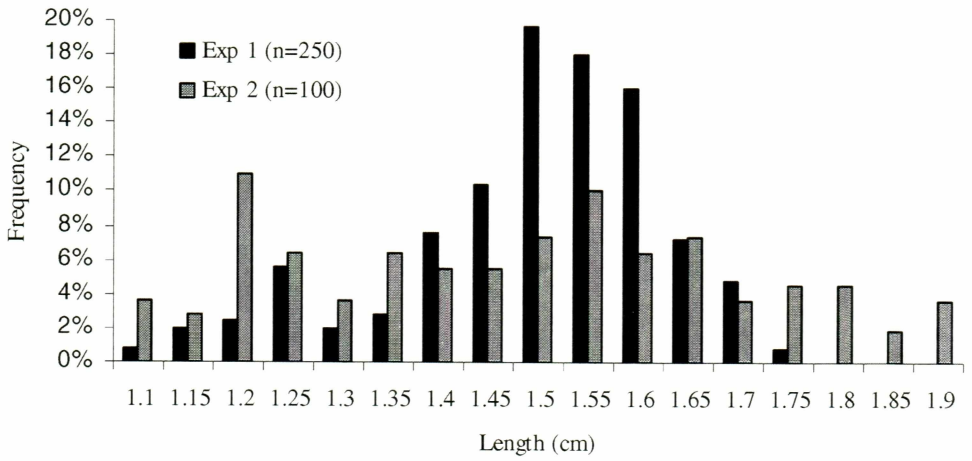

Fig. 3.5 Initial length-frequency distribution of *O. litoralis* in experiment 1 (Exp 1) and experiment 2 (Exp 2).

Table 3.2 *O. litoralis* initial and final wet weights, growth and molting rates in all treatments for experiments 1 (Exp 1) and 2 (Exp 2). Wet weight (WW) and growth rates reported as mean±SD). *control molting rate reported for weeks 1-3 only

Exp.	Treatment	T (°C)	Initial amphipod WW (mg), n=50 per treatment	% of amphipods that molted	Final amphipod WW (mg), n=45	Mean growth rate (mg/day)
1	High $\delta^{13}C$	1	51.9±13.6	72	64.5±19.3	0.4±0.5
1	High $\delta^{13}C$	4	54.6±12.0	82	68.8±14.8	0.6±0.6
1	Moderate $\delta^{13}C$	1	54.4±10.4	78	66.5±15.9	0.4±0.5
1	Control	1	56.3±12.7	22*	68.8±13.8	0.4±0.8
1	Fasting	1	55.0±11.1	36	60.8±16.6	0.2±0.9
2	High $\delta^{13}C$	1	54.9±28.1	31	57.1±26.9	0.0±0.1
2	Control	1	55.6±21.8	20	57.0±21.7	0.0±0.1

in September. Most amphipods in fed treatments in Exp 1 underwent a single molt cycle (72 to 82%); fewer amphipods molted in Exp 2 (20 and 31%; Table 3.2). Amphipods in the fasting treatment also gained weight and molted, but at a slower rate than those in the fed treatments in Exp 1.

Mortality during both experiments was low, between 2 and 4% in all treatments. At least one animal in each tank survived until sampling, so no replicates were lost. Growth rates were similar among the fed treatments in Exp 1, ranging between 0.4 (±0.8) and 0.6 (±0.6) mg WW d^{-1}. There was no significant difference between the two temperatures when comparing mean growth rates throughout the experiment (t-test, p=0.310). By the final week, amphipods maintained at the higher temperature had gained a higher percentage of weight (59.7 (±28.1) %) compared to those at 1°C (33.3 (±11.1) %), but again, the difference was not significant (t-test, p=0.075). Amphipods in Exp 2 showed a significantly lower mean growth rate of 0.0 (±0.1) mg WW d^{-1} compared to the mean growth rates in fed treatments in Exp 1 (0.4 (±0.8) to 0.6 (±0.6) mg WW d^{-1}, t-test, p<0.001). Growth rates for small (<60 mg WW: 0.1±0.1 mg WW d^{-1}) and large amphipods (>60 mg WW: 0.0±0.1 mg WW d^{-1}) were not significantly different (t-test, p=0.529). There was also no difference in growth rate between the control and the enriched treatment in Exp 2 (t-test, p=0.423).

3.2.2 *Carbon and nitrogen turnover*

Mean initial stable isotope values of the amphipods within individual treatments in Exp 1 ranged from –22.0 (±1.0) to –20.7 (±1.6) ‰ for $\delta^{13}C$ and from 14.1 (±0.5) to 12.5 (±0.5) ‰ for $\delta^{15}N$ (Table 3.3). Mean initial amphipod values in Exp 2 were –20.1 (±0.9) $\delta^{13}C$ and 15.4 (±0.5) $\delta^{15}N$ for the control and –19.5 ‰ (±1.2) $\delta^{13}C$ and 15.9 (±0.6) ‰ $\delta^{15}N$ for the highly enriched treatment. The $\delta^{13}C$ and $\delta^{15}N$ of the amphipods approached asymptotic values toward the end of the nine week experiment in all fed treatments in Exp 1; however, asymptotic values were on average approximately 10‰ below the $\delta^{13}C$

Table 3.3 Initial and final experimental amphipod $\delta^{13}C$ and $\delta^{15}N$ values for experiments 1 (Exp 1) and 2 (Exp 2). t_0 = initial isotope value, t_f = final isotope value, (n=5 for all samples). Values reported as mean±SD.

Exp	Treatment	T (°C)	$\delta^{13}C$ Amphipod(t_0) (‰)	$\delta^{13}C$ Amphipod (t_f) (‰)	$\delta^{15}N$ Amphipod(t_0) (‰)	$\delta^{15}N$ Amphipod (t_f) (‰)
1	High $\delta^{13}C$	1	-22.0±1.0	8.0±4.8	13.2±0.8	10.6±0.4
1	High $\delta^{13}C$	4	-20.7±1.6	10.3±4.7	13.1±0.8	9.7±0.2
1	Moderate $\delta^{13}C$	1	-21.8±1.2	-18.0±0.7	14.1±0.5	10.6±0.4
1	Fasting	1	-21.7±1.5	-21.4±1.1	13.2±0.4	14.1±0.7
1	Control	1	-22.0±0.9	-22.9±0.6	12.5±0.0	11.4±0.6
2	High $\delta^{13}C$	1	-19.5±0.9	7.9±14.4	15.9±0.6	19.6±0.3
2	Control	1	-20.1±1.2	-20.8±0.7	15.4±0.5	12.3±0.4

Table 3.4 Fractional (c) and metabolic (m) turnover rate constants for experiments 1 (Exp 1) and 2 (exp 2). Fractional turnover rate constants estimated using the model from Tieszen et al. 1983. Half-lives were calculated using the equation, half-life=ln (0.5)/c. Metabolic turnover rate (m) constants were estimated using the model from Hesslein et al. (1993) and are the relative contribution of metabolic tissue replacement to the total observed isotopic change (fractional turnover) in *O. litoralis*. Growth rates (g) were calculated according to Hesslein et al. (1993).

Exp	Treatment	Element	Diet	T (°C)	c ± SE (d^{-1})	Half-life (d)	m ± SE (d^{-1})	g ± SE (mg d^{-1})
1	High $\delta^{13}C$	$\delta^{13}C$	1	1	0.037±0.009	18.7	0.033±0.003	0.007±0.001
1	High $\delta^{13}C$	$\delta^{13}C$	1	4	0.050±0.012	13.9	0.042±0.005	0.009 ±0.001
1	High $\delta^{13}C$	$\delta^{15}N$	1	1	0.031±0.013	22.4	0.024±0.003	0.007±0.001
1	High $\delta^{13}C$	$\delta^{15}N$	1	4	0.031±0.013	22.4	0.023±0.003	0.009 ±0.001
1	Moderate $\delta^{13}C$	$\delta^{15}N$	2	1	0.034±0.013	20.4	0.026±0.003	0.008 ±0.001
2	High $\delta^{13}C$	$\delta^{13}C$	1a	1	0.009±0.002	77.0	0.008±0.001	0.002±0.000
2	High $\delta^{13}C$	$\delta^{15}N$	1a	1	0.006±0.001	115.5	0.004±0.000	0.002±0.001

values of the enriched diets. Amphipods in Exp 2 did not reach asymptotic values by the end of the ten weeks.

From Equation 1 (Tieszen et al. 1983), estimated fractional turnover rate constants (c) for the highly enriched treatments were 0.050 (±0.012) d^{-1} at 4°C and 0.037 (±0.009) d^{-1} at 1°C for carbon, and 0.031 (±0.013) d^{-1} for nitrogen at both temperatures (Table 3.4). Corresponding carbon half-lives (HL) were 13.9 and 18.7 days for 4°C and 1°C, respectively, and 22.4 days for nitrogen. Amphipods at 4°C showed faster carbon turnover (Fig. 3.6a-d) compared to the 1°C observations, but the difference was not significant (likelihood ratio, χ^2=4.778, p=0.114). While the high data variability did not allow an estimation of the carbon turnover rates for diet 2, the nitrogen turnover was very similar to the two highly enriched treatments (c = 0.034±0.013 d^{-1}, HL = 20.4 days). The control group that received non-enriched (in $\delta^{13}C$) diet for the first three weeks of Exp 1 exhibited constant $\delta^{13}C$ values (Fig. 3.6a).

Fasting amphipods exhibited little change in $\delta^{13}C$ over the course of the experiment (Fig. 3.6g), while the $\delta^{15}N$ data showed a 3.3‰ enrichment from week 1 (12.6 (±1.1) ‰ to week 5 (15.9 (±3.2) ‰, Fig. 3.6h). A linear regression of the $\delta^{15}N$ change over time showed a significant increase (r^2=0.34, p<0.0001) from weeks 1 to 5, but no change was detected in $\delta^{15}N$ from week 6 through the end of the experiment (r^2=0.09, p=0.07).

In Exp 2, amphipods did not equilibrate with diets 1 and 3 during the ten-week experiment (Fig. 3.7a, b, d), evidence that both carbon and nitrogen turnover were slower for amphipods collected in September. It is important to note that variability was greater in Exp 2, and the data did not fit the exponential models as well as in Exp 1. Thus, the confidence in the estimated rate constants for Exp 2 is low. However, they are reported here for comparison to Exp 1, and to illustrate the magnitude of difference in fractional turnover rates between the two experiments. The estimated carbon turnover rate for the highly enriched treatment (c = 0.009 (±0.002) d^{-1}, HL = 77.0 days) was 75% slower than

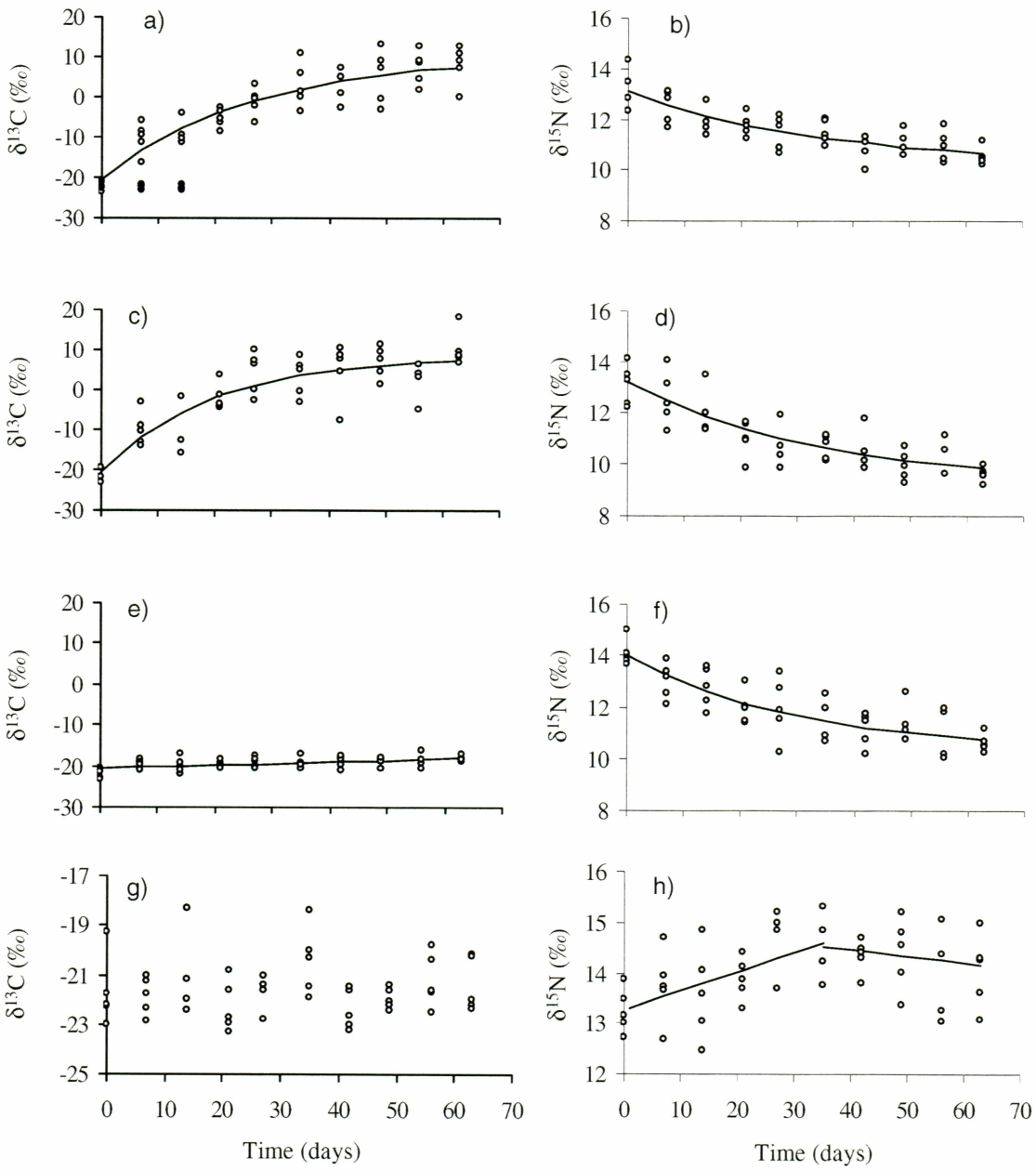

Fig. 3.6 Changes in $\delta^{13}C$ and $\delta^{15}N$ as a function of time in Experiment 1. a) $\delta^{13}C$, diet 1(open circles) and diet 3 (closed circles), T=1°C. The control group (diet 3) ran until week 3, when the diet was accidentally switched to diet 1. b) $\delta^{15}N$ diet 1, T=1°C, c) $\delta^{13}C$ and d) $\delta^{15}N$ diet 1, T=4°C, e) $\delta^{13}C$ and f) $\delta^{15}N$ diet 2, T=1°C, g) $\delta^{13}C$ and h) $\delta^{15}N$ no food, T=1°C. For a-f, lines represent best fit nonlinear regression. For fasting $\delta^{15}N$ plot, lines represent separate least squares linear regression for weeks 1-7 and 7-9. Note the y-axis scale was expanded in plots g and h to better show stable isotopic dynamics during fasting.

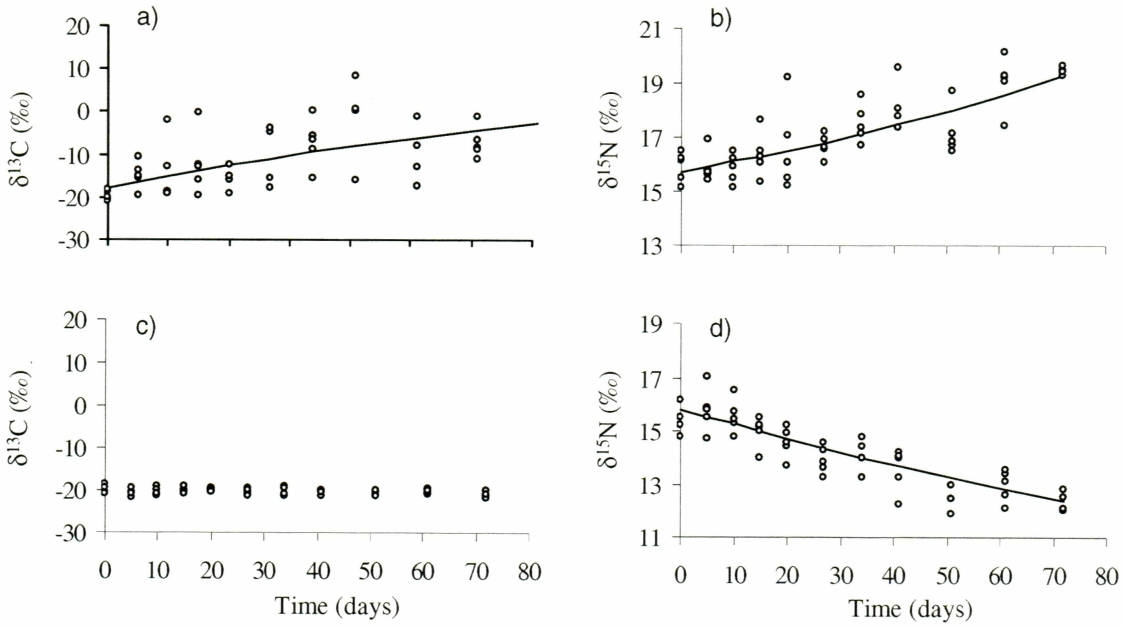

Fig. 3.7 Changes in $\delta^{13}C$ and $\delta^{15}N$ as a function of time in Experiment 2. a) diet 1a, $\delta^{13}C$, b) diet 1a, $\delta^{15}N$, c) diet 3, $\delta^{13}C$, d) diet 3, $\delta^{15}N$. Lines represent best fit nonlinear regression. Turnover rates calculated for a and d only.

carbon turnover in Exp 1 at the same temperature. Amphipods receiving the highly enriched diet did not approach an asymptotic $\delta^{15}N$ value; therefore a nitrogen turnover rate could only be calculated for the control group (c = 0.006 (±0.001) d^{-1}, HL = 115.5 days). Amphipods receiving the non-enriched diet as a control maintained constant $\delta^{13}C$ values, with less than 0.8‰ difference between the initial (–20.1 (±0.9) ‰) and the final (–20.8 (±0.7) ‰) mean $\delta^{13}C$ (Fig. 3.7c).

Using Equation 2 (Hesslein et al. 1993), metabolic turnover rate constants (m) in Exp 1 ranged from 0.033 (±0.003) to 0.042 (±0.005) d^{-1} for $\delta^{13}C$ and from 0.023 (±0.003) to 0.026 (±0.003) d^{-1} in $\delta^{15}N$ (Table 3.4). Relative to total isotopic change (g+m), metabolic turnover was responsible for 84 to 89% of the observed change in carbon and 74 to 77% of the observed isotopic change in nitrogen in Exp 1 (Fig. 3.8). Metabolic turnover rates were faster at 4°C than at 1°C carbon, and nitrogen showed no difference between the two temperatures. Amphipods in Exp 2 showed slower metabolic turnover, with a carbon turnover rate constant of 0.008 (±0.001) d^{-1} and 0.004 (±0.000) d^{-1} for nitrogen; however, total observed isotopic change was also slower, and the relative contribution of metabolic turnover was similar to Exp 1, accounting for 89% of carbon and 67% of nitrogen turnover in Exp 2 (Fig. 3.9).

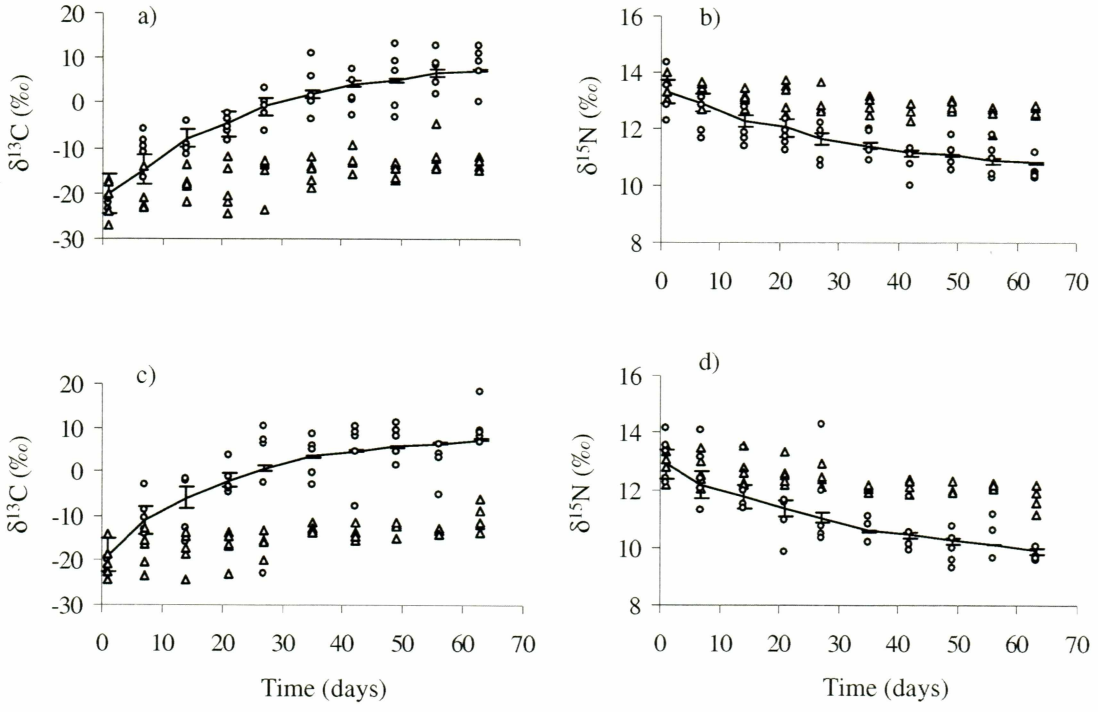

Fig. 3.8 Relative contribution of metabolic turnover to isotopic change in Experiment 1. Plots are for treatments receiving the highly enriched diet (diet 1); a) $\delta^{13}C$, 1°C, b) $\delta^{15}N$, 1°C, c) $\delta^{13}C$, 4°C, d) $\delta^{15}N$, 4°C. Experimental observations (circles) plotted with predicted data points based on growth alone (=no metabolic turnover, triangles). Lines represent theoretical curves describing fractional turnover (=growth + metabolic turnover). Lines are fit through means of five theoretical data points calculated using the model from Hesslein et al. (1993). Error bars are SD.

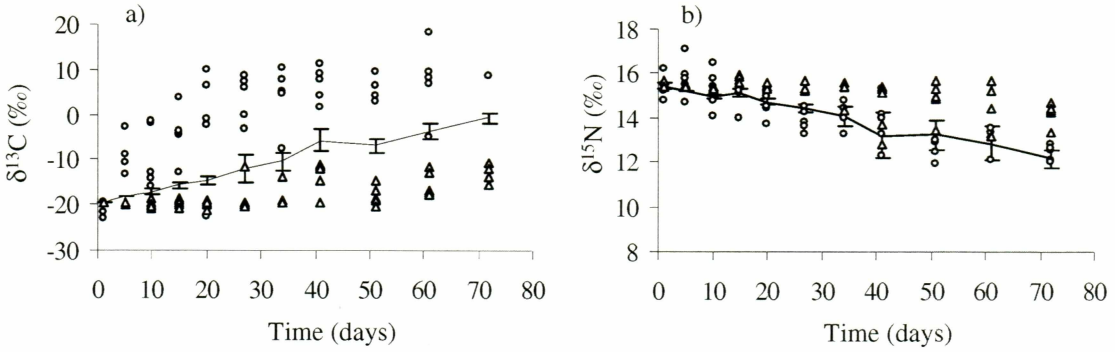

Fig. 3.9 Relative contribution of metabolic turnover to isotopic change in *O. litoralis* in Experiments 2 (Exp 2). a) $\delta^{13}C$, 1°C, highly enriched diet (diet 1a) treatment and b) $\delta^{15}N$, 1°C, control. Experimental observations (circles) plotted with predicted data points based on growth alone (=no metabolic turnover, triangles). Lines represent theoretical curves describing fractional turnover (=growth + metabolic turnover). Lines are fit through means of five theoretical data points calculated using the model from Hesslein et al. (1993). Error bars are SD.

4. Discussion

Stable isotopes are increasingly being used to investigate trophic interactions in the Arctic (Hobson and Welch 1992, Hobson et al. 1995, Iken et al. 2005) and Southern Ocean (Frazer et al. 1996, Schmidt et al. 2003) where sea ice algal production provides seasonal food sources, resulting in diet switching among marine fauna that utilize this production. Examples include the dominant copepod *Calanus glacialis* that relies primarily on ice algae for its nutrition during ice covered periods in Hudson Bay (Runge and Ingram 1988) and the dominant Antarctic copepod *Stephos longipes* that utilizes ice algae prior to the phytoplankton bloom in the austral spring (Schnack-Schiel 2003). Despite wide use of stable isotope techniques, few laboratory studies have calibrated isotope turnover in the organisms that rely on these resources. This study provides the first isotopic change and metabolic turnover rates for an Arctic marine invertebrate.

4.1 Methodological constraints

Fry and Arnold (1982) found that the natural isotopic variability in brown shrimp and the analytical error associated with isotope measurements at that time limited their ability to estimate metabolic turnover. Despite advancements in the technology, a similar problem was encountered in this study. The moderately enriched diet 2 in Exp 1 was 3-5‰ $\delta^{13}C$ more enriched than initial amphipod values, but this difference was overwhelmed by the natural and experimental variability of amphipod $\delta^{13}C$ values. Hence, carbon turnover rate could not be calculated for this treatment. Fry and Arnold (1982) therefore suggested using experimental diets that are even more different from the initial value of the experimental organism to overcome this problem. For an opportunistic omnivore like *O. litoralis* (Carey and Boudrias 1987), natural variability can be high due to broad individual diet selection and feeding opportunities in the field. In this study, field collected *O. litoralis* had $\delta^{13}C$ with a difference of 1.4-2.6‰ between individual animals within each sampling period. In the diet switch experiments, a difference between initial amphipod values and diet greater than 5‰ ($\delta^{13}C$) was necessary to clearly show carbon

isotope dynamics in this species. The initial amphipod-diet difference in $\delta^{15}N$ was greater than 10‰ in all experiments and was sufficient to overcome the natural and experimental variability of *O. litoralis*, which was similar to that reported for $\delta^{13}C$.

The experimental diets used in this study were composed of two main components: enriched ice algae and a commercial algal-based fish food. This might explain the low (by approximately 10‰ relative to the diet) final $\delta^{13}C$ values reached by the experimental amphipods receiving the highly enriched diets and suggests that the full enrichment of the feed may not have been available to the amphipods. The loss of enrichment could have been caused by leaching of inorganic ^{13}C that was not rinsed from the ice algal cells following the enrichment incubations or by differential assimilation rates among the feed components via selective feeding, or assimilation processes. These results highlight the advantage of using a single component experimental diet, as recently suggested by Yokoyama et al. (2005).

In diet switch experiments, final equilibrium values are typically determined by adding a fractionation factor to the value of the diet. In this study, final equilibrium $\delta^{13}C$ and $\delta^{15}N$ values were obtained by fitting Eq. 1 to the data and estimating the asymptotic values being approached by the amphipods (δ_f). There is an advantage to this procedure. Though there are generally accepted ranges, carbon and nitrogen fractionation rates vary between individual consumers and can be unpredictable because they are affected by factors such as food type and physiological state (McCutchen et al. 2003, Yokoyama et al. 2005). Using experimentally determined end equilibrium values avoids the necessity of assigning arbitrary fractionation factors. In addition, Fry and Arnold (1982) found good agreement between end equilibrium estimates from fitted data and estimates from diet values with added fractionation factors.

4.2 Turnover rates

Stable isotopic change in a consumer following a diet switch results from growth, as tissues synthesized from the new diet are added, and from metabolic turnover, as tissues synthesized from the previous diet are replaced with tissues synthesized from the new diet (Bosley et al. 2002). Only a handful of studies have investigated the contribution of metabolic turnover to isotopic change in invertebrates, and of these most have focused on rapidly-growing larval and post-larval life stages for which growth was the primary mechanism driving isotopic change. In a pioneering study, Fry and Arnold (1982) determined carbon turnover in larval brown shrimp that doubled in weight in 8 to 23 days and concluded that metabolic turnover in invertebrates is tied primarily to growth rather than to maintenance metabolism. Because isotopic change was driven by dilution effects during the production of new tissue, Fry and Arnold (1982) reported carbon turnover in terms of growth. This turnover model has subsequently been used for various invertebrate and fish species, all exhibiting rapid growth (Fry and Arnold 1982, Herzka and Holt 2000, Bosely et al. 2002, Jardine et al. 2004, Logan et al. 2006). *O. litoralis* in this study grew slowly in the feeding experiments compared to the target species in the studies listed above, increasing initial body weight by 32 to 59% in nine weeks in the spring and by less than 10% in ten weeks in autumn. Yet, in both experiments, relatively rapid isotopic change was observed. In the current study, isotopic change was highly correlated with time since the diet switch, suggesting that isotopic change was tied closely to maintenance metabolism. Because of this, an approach so far used only for endotherms and a few slow-growing fish species was used to report isotopic change in *O. litoralis* as a function of time rather than growth (Tieszen et al. 1983, Hesslein et al 2002).

Half-lives obtained from our Arctic amphipods in early spring (13.9 to 18.7 days for $\delta^{13}C$ and 22.4 days for $\delta^{15}N$) are within the range of those found for rapidly-growing Japanese temperate bass *Lateolabrox japonicus* juveniles reared between 18 and 25°C with carbon and nitrogen half-lives of 19.3 to 25.7 days (Suzuki et al. 2004, Table 4.1a and b), rapidly

Table 4.1a Published fractional and metabolic turnover rates for comparison. Fractional turnover constants calculated according to Tieszen et al. (1983) and metabolic turnover constants calculated according to Hesslein et al. (1993). * indicates half-life values not published in original literature that were calculated here for comparison (HL = ln(0.5)/c, where c is the isotopic change constant including change attributed to both growth and metabolic turnover). ‡ indicates value calculated using published growth rate constants (k) with the equation; growth (doubling time) = ln 2 /k. § indicates values estimated from published plots in original literature references. BW = body weight.

Organism	T (°C)	Growth (doubling time) (days)	Fractional turnover constant c (d^{-1})		Half-life (days)		Metabolic turnover constant m (d^{-1})		Study
			C	N	C	N	C	N	
Krill (*Euphausia superba*)	-1.5	140	-	-	-	-	0.000	0.001	Frazer et al. 1997
Krill (*Euphausia superba*)	1.5	70	-	-	30.4*	25*	0.007	0.004	Frazer et al. 1997
Amphipod (*Onisimus litoralis*; spring)	1.0	180	0.037	0.013	18.7	22.4	0.033	0.024	This study
Amphipod (*Onisimus litoralis*; spring)	4.0	130	0.050	0.013	13.9	22.4	0.042	0.023	This study
Amphipod (*Onisimus litoralis*; autumn)	1.0	>300	0.009	0.006	77.0	115.5	0.008	0.004	This study
Snail (*Tarebia granifera*)	20-27	-	-	0.034	-	20.2	-	-	McIntyre and Flecker 2006
Snail (*Lavigeria grandis*)	25-27	-	-	0.014	-	49.5	-	-	McIntyre and Flecker 2006
Tadpole (*Rana palmipes*)	20-27	-	-	0.005	-	138.6	-	-	McIntyre and Flecker 2006
Catfish (*Ancistrus triradiatus*)	20-27	-	-	0.038	-	18.2	-	-	McIntyre and Flecker 2006
Flounder (*Paralichthys olivaceus*; mean BW 0.26g)	14.8-18.9	3-7	0.04-0.05	-	14-17*	-	-	-	Tominaga et al. 2003
Flounder (*Paralichthys olivaceus*; mean BW 1.06g)	14.8-18.9	<6	0.14	-	5.0	-	-	-	Tominaga et al. 2003
Bass (*Lateolabrax japonicus*)	23	35‡	0.033	0.036	21.0	19.3	-	-	Suzuki et al. 2005
Salmon (*Oncorhynchus nerka*; BW 9 to 15g)	10-13	26.7 ‡	-	0.048	-	14.4*	-	-	Sakano et al. 2005
Salmon (*Oncorhynchus nerka*; BW 71 to 170g)	10-13	86.6 ‡	-	0.040	-	17.3*	-	-	Sakano et al. 2005
Salmon (*Oncorhynchus nerka*; BW 169 to 308g)	10-13	231.0 ‡	-	0.017	-	40.8*	-	-	Sakano et al. 2005
Salmon (*Salmo salar*)	-	69.3‡	-	-	71.9	-	0.008	-	Jardine et al. 2004
Salmon (*Salmo salar*)	-	86.6 ‡	-	-	21.9	-	0.020	-	Jardine et al. 2004
Salmon (*Salmo salar*)	-	173.3 ‡	-	-	19.2	-	0.022	-	Jardine et al. 2004
Goby (*Rhinogobius* sp.)	-	>30§	-	-	-	33 – 99*	-	0.002 – 0.006	Maruyama et al. 2001
Catfish (*Ictalurus furcatus*)	11 - 19	77-187.5 ‡	<0.004	<0.004	>173*	>173*	-	-	MacAvoy et al. 2001
Whitefish (*Coregonus nasus*)	10	100-250§	-	-	-	-	0.0018	0.0018	Hesslein et al. 1993
Gerbil (*Meriones unguienlatus*)	-	-	0.025	-	27.6	-	-	-	Tieszen et al. 1983
Mouse (*Mus musculus*)	-	-	0.029	0.027	23.9	25.7	0.027	0.025	MacAvoy et al. 2005
Quail (*Coturnix japonica*)	-	-	0.056	-	24.4	-	0.056	-	Hobson and Clark 1992

Table 4.1b Published fractional turnover rates and metabolic turnover coefficients for comparison. Fractional turnover constants calculated according to Tieszen et al. (1983). Metabolic turnover rate coefficients calculated as relative contribution to total isotopic change according to Fry and Arnold (1982). A value of -1.0 or greater indicates no metabolic turnover. Metabolic turnover commences at values less than -1.0, and becomes more rapid with decreasing values. Metabolic turnover constants in bold indicate that they are significantly lower than –1. Metabolic turnover constants were calculated for *O. litoralis* for comparison by determining *O. litoralis* weight at isotopic half-life and applying the equation: $c = \log(0.5)/\log(w_t/w_i) - 1$, where c = metabolic turnover constant according to Fry and Arnold (1982), w_i is the initial weight and w_t is the weight at sampling. Original equations found in Fry and Arnold (1982). * indicates half-life values not published in original literature that were calculated here for comparison (HL = ln(0.5)/c, where c is the isotopic change constant including change attributed to both growth and metabolic turnover). § indicates values estimated from published plots in original literature references.

Organism	T (°C)	Growth (doubling time) (days)	Fractional turnover constant c (d^{-1})		Half-life (days)		Metabolic turnover coefficient (unitless)		Study
			C	N	C	N	C	N	
Shrimp (*Penaeus aztecus*)	23-25	3.5	-	-		-	**-1.94**	-	Fry and Arnold 1982
Shrimp (*Penaeus aztecus*)	23-25	8-23	-	-		-	**-1.45 to –2.27**	-	Fry and Arnold 1982
Amphipod (*Onisimus litoralis*; spring)	1.0	>70	0.037	0.013	18.7	22.4	**-5.44**	**-4.98**	This study
Amphipod (*Onisimus litoralis*; spring)	4.0	>70	0.050	0.013	13.9	22.4	**-5.64**	**-4.64 / -4.98**	This study
Amphipod (*Onisimus litoralis*; autumn)	1.0	>100	0.009	0.006	77.0	115.5	**-4.80**	**-4.35**	This study
Drum (*Sciaenops ocellatus*)	24	1-2§	-	-	<2	<2	-1.12	-0.94	Herzka and Holt 2000
Drum (*Sciaenops ocellatus*)	28	1-2 §	-	-	<2	<2	-0.96 / –1.96	-0.99 / –1.13	Herzka and Holt 2000
Flounder (*Pseudopleuronectes americanus*)	13	<8§	0.17	0.18	4.1	3.9	-0.79	-1.0	Bosely et al. 2002
Founder (*Pseudopleuronectes americanus*)	18	<8 §	0.32	0.22	2.2	3.1	-1.34	-1.14	Bosely et al. 2002
Mummichog (*Fundulus heteroclitus*)	18	35-105‡	-	-	-	-	-	**-2.33**	Logan et al. 2006
Flounder (*Paralichthys dentatus*; larvae)	13	<2	0.08	0.09	9.2	7.5	**-1.4**	**-1.7**	Witting et al. 2004
Flounder (*Paralichthys dentatus*; larvae)	22	<3	0.24	0.22	2.9	3.2	**-1.6**	**-1.4**	Witting et al. 2004
Flounder (*Paralichthys dentatus*; young juvenile)	13	<4	0.06	0.05	11.6	13.6	-1.2	-1.0	Witting et al. 2004
Flounder (*Paralichthys dentatus*; young juvenile)	22	<2	0.14	0.11	5.0	6.1	-1.2	-1.0	Witting et al. 2004
Flounder (*Paralichthys dentatus*; older juvenile)	13	<9	0.04	0.01	16.9	70*	**-2.6**	-0.1	Witting et al. 2004
Flounder (*Paralichthys dentatus*; older juvenile)	22	<8	0.12	0.01	6.0	70*	**-5.9**	-0.6	Witting et al. 2004

growing post-larval brown shrimp (carbon half-life 4 to 19 days, Fry and Arnold 1992), and adult mouse muscle (carbon half-life 23.9 days, MacAvoy et al. 2005).

The rapid isotopic change observed in Exp 1 in this study resulted primarily from metabolic tissue replacement. The metabolic turnover rate constants found in Exp 1 (0.033 to 0.042 d^{-1} for $\delta^{13}C$ and 0.023 to 0.026 d^{-1} for $\delta^{15}N$) are high compared to other ectothermic taxa, particularly in light of the slow growth rates and low ambient temperatures (Table 4.1a and b). *O. litoralis* turnover rate constants are within the range of those found for salmon smolts *Salmo salar* (0.008 to 0.022 d^{-1} for $\delta^{15}N$, no data for $\delta^{13}C$) that were reported to be the fastest to date for any ectotherm (Jardine et al. 2004).

Fry and Arnold (1982) suggested that metabolic turnover would be more important in slower- versus faster-growing organisms. The results found here for *O. litoralis* support this hypothesis when compared to rapidly growing organisms, for which isotopic change is primarily driven by growth and metabolic turnover is relatively unimportant. In addition, compared to Antarctic krill (*E. superba*) reared at 1.5°C that grew twice as fast as *O. litoralis* in this study, metabolic turnover rates were more than an order of magnitude higher for slower-growing *O. litoralis* (Table 4.1a).

Despite the lower growth rates and fractional turnover rates observed in Exp 2, the relative contribution of metabolic turnover to total isotopic change was similar to that in Exp 1. While metabolic turnover rate constants were more than an order of magnitude lower in Exp 2, metabolic turnover accounted for 75 and 50% of carbon and nitrogen fractional turnover, respectively. In Exp 1, metabolic turnover accounted for 67-77% change in carbon and 55-67% change in nitrogen. Therefore, within this experiment, slower growth in autumn did not necessarily correspond to a higher contribution from metabolic turnover as has been previously suggested (Fry and Arnold 1992, Maruyama et al. 2001).

4.3 Growth and mortality

The rate of isotopic change was nearly an order of magnitude slower in amphipods collected in autumn compared to those collected in the spring. This difference can partially be explained by the very slow growth rates in the autumn-collected specimens, also an order of magnitude lower than in March. Higher growth rates in the spring likely relate to an abundant food source after the winter food dearth. These findings agree with previous life cycle studies in that the fastest growth rates for *O. litoralis* in the southwestern Beaufort Sea occurred in late May at the peak of ice algal production (Boudrias and Carey 1988). Possible causes for the slower growth rates in the autumn experiment include life history or environmental factors. Not all amphipods in the second experiment were of the same age class. Length-frequency distributions from Boudrias and Carey (1988) suggest that Exp 1 amphipods collected in March were all from the same second year immature cohort, while the wider size range of amphipods collected in September (Exp 2) were likely a mix of the same cohort and first year juveniles released in the spring. The majority, according to body length, were older immature animals (1.0 to 1.7 cm) that would be preparing for mating and reproduction under the winter sea ice (Boudrias and Carey 1988). Low growth rates could result from energy being routed towards gonad development rather than somatic growth in these animals (Glazier 1999). However, growth rates were nearly as slow for the smallest amphipods that would overwinter as young immature animals, not reaching adulthood until the following autumn. Alternatively, Antarctic krill (*E. superba*) have been shown to reduce their metabolism in winter as an energy saving strategy (Attkinson et al. 2002). The transfer from Arctic summer field conditions (24 hour daylight and 9°C seawater temperatures) to laboratory conditions (24 hour darkness and 1°C seawater) in Exp 2 may have triggered such a response in *O. litoralis*, however, there is no evidence that other *Onisimus* species employ this strategy (Werner and Auel 2005). Another possibility is that slower growth rates occurred in autumn as a result of seasonal temperature acclimatization. Ectotherms can acclimate to seasonal temperature regimes, decreasing lethal temperatures in winter and increasing them in summer (Schmidt-Nielsen 1997).

This strategy can be especially useful in nearshore polar species like *O. litoralis* that experience a wide range of seasonal temperatures (–1.8 to 9.0°C, Table 3.1) while remaining active throughout the year. In September, the experimental amphipods were acclimated to approximately 9°C in the field when they were moved to 1°C experimental conditions. Adjustment of metabolism to a new ambient temperature takes much longer for a warm-acclimated animal moved to a colder temperature than for cold-acclimated animal moved to warmer environment (Schmidt-Nielsen 1997). A cold-induced reduction in metabolism may have resulted in lower growth rates.

The massive mortality that occurred during transport from the field and in the laboratory in the week prior to the start of Exp 2 indicates that the amphipods collected at that time were in poorer physical condition than those collected in the spring. Amphipods were collected from Elson Lagoon in September, when seawater temperatures were 9°C. Along the Chukchi coast this species can escape the warm summer surface temperatures by migrating to deeper water. In contrast, the amphipods in the shallow lagoon were unable to move vertically to colder water and may have been thermally stressed and in poor physical condition prior to capture. This is supported by the C/N values in the Elson Lagoon amphipods, which were significantly lower than in amphipods collected during all other sampling periods from the Chukchi Sea (6.1 (±0.2) for September versus 7.4 (±0.3), 7.6 (±0.1), and 7.0 (±0.2) for March, May, and December, respectively, $p<0.001$). Low C/N values may indicate a low ratio of carbon rich lipid to other body tissues and have been used as a proxy for lipid content (Perga and Gerdoux 2005). Some polar invertebrates use the productive summer season to grow and build up energy stores in preparation for over wintering and reproduction (Percy 1993, Lee et al. 2006), and low lipid stores in September may be a further indication of physiological stress.

4.4 Temperature effects on isotopic change

Growth and metabolism in marine invertebrates are affected by ambient temperature (Hochachka and Somero 2002). *In situ* temperatures under spring sea ice are lower than

the experimental temperatures in this study, typically near the freezing point of seawater (–1.6 to –1.8°C). Frazer et al. (1997) found that krill reared at –1.5°C showed significantly slower carbon turnover than at 1.5°C, however, krill have also been shown to have a narrow physiological temperature tolerance (McWhinnie 1964). Temperatures in offshore Antarctic waters are very stable, ranging from –1.96° to 1.64°C year round (Robertson et al. 2001). *O. litoralis* experience a wider range of seasonal temperatures in shallow coastal Arctic waters (see Table 3.1), suggesting that they are more flexible in their temperature tolerance. No significant temperature effect on either growth or turnover rate was observed in the current study; however, a trend toward slower growth and slower carbon turnover in amphipods maintained at 1.0°C compared to those at 4°C suggests that both processes are temperature sensitive in this species. Therefore, *in situ* carbon turnover rates in amphipods feeding under the ice in spring will likely be slower than those experimentally estimated for 1°C. Spring *in situ* turnover rates can be approximated using the Q_{10} relationship between temperature and carbon turnover (Schmidt-Nielsen 1997). Using a Q_{10} of 2.69 calculated for carbon turnover between the experimental temperatures 1 and 4°C, a carbon half-life of 24.6 days would be expected at –1.8°C, less than six days slower than at 1°C.

4.5 Fasting

Starving or fasting animals can show a progressive enrichment in ^{13}C or ^{15}N as the lighter isotopes are preferentially excreted in the catabolism of body tissues (Hobson et al. 1993, Gannes et al. 1997). In this study, no changes were observed in $\delta^{13}C$ over the nine week period. These results are consistent with previous studies on fish (*Salmo salar*, Jardine et al. 2004), mysids (*Mysis mixta* and *Neomysis integer*, Gorokhova and Hansson 1999), and krill (*E. superba*, Frazer et al. 1997). Unlike $\delta^{13}C$, $\delta^{15}N$ became enriched over the first half of the experiment. The significant 3.3‰ enrichment in $\delta^{15}N$ during the first five weeks of our experiment, and the subsequent flattening of the curve, may indicate delayed conservation of somatic nitrogen after a prolonged period without food. After two weeks without food, the Arctic amphipod *Themisto libellula* decreased its

consumption of internal energy stores by 70 to 75% and continued to conserve energy through the subsequent two weeks (Percy 1993). Such a conservation strategy, employed after five weeks without food, could have stabilized the $\delta^{15}N$ in the tissues of *O. litoralis* and would explain why there was no change in $\delta^{15}N$ from day 35 through the end of the experiment.

4.6 Field applications

Growth and metabolic turnover rates in the present study show that a diet switch could be detected in the tissues of *O. litoralis* within two to three weeks in the spring, given that there is sufficient difference in isotope composition between the diets. The slower fractional turnover rates observed in *O. litoralis* collected in September suggests that stable isotopes will integrate their diet composition over a period of months and reduce the temporal resolution when using stable isotopes to monitor diet changes in the field in autumn. However, it is unlikely that growth would naturally be halted several months prior to winter, a time when similar Arctic amphipods, including two sympagic *Onisimus* species, (*O. nanseni* Sars and *O. glacialis* Sars), continue to grow and mature (Collie 1985, Arndt and Beuchel 2006). Therefore, the low growth rates in Exp 2 probably resulted in underestimates of late summer *in situ* turnover rates for *O. litoralis*.

No ice algal stable isotopic enrichment was detected in this study between March and early May 2004. Ice algae become enriched in ^{13}C when CO_2 concentrations within the brine channel network become limiting, a situation that requires high biomass and productivity (Kennedy et al. 2002, Thomas and Dieckmann 2003). This situation has been found in recent studies in the Arctic (Schubert and Calvert 2001, Hobson et al. 2002, Søreide et al. 2006), and Antarctic (Gibson et al. 1999, Kennedy et al. 2002, Schmidt et al. 2003) where ice algae were isotopically heavier than phytoplankton. However, when productivity and biomass are low, demand for CO_2 is not sufficient to draw concentrations down to levels that result in enrichment. A similar situation was found in offshore Arctic pack ice (Iken et al. 2005). Sea ice chl *a* and POC values in our

study, specifically in May, were more than two orders of magnitude lower than had been measured at the same location in the previous two years (Gradinger and Bluhm 2005), indicating that the highly productive spring bloom that typically starts in March and extends through the onset of ice melt in June had not, or had not yet, occurred in the sampling area. Abiotic factors including light, temperature, salinity, and nutrient availability control the development of the ice algal community; however, in early spring light is the major controlling factor of algal productivity (Ambrose et al. 2005 and references therein). Snow cover, ice thickness, and sediment entrained during ice formation can affect light availability in the bottom-most decimeter of the ice where temperature and nutrient conditions are most favorable for algal growth. In May 2004, snow and ice depth were similar to previous years, however, a visible sediment layer was found in the ice at the study site. Entrained sediment is a common feature in Arctic sea ice (Kempema et al. 1989, Frey et al. 2001). In the shallow Arctic shelf waters, autumn storms cause seafloor sediments to become suspended in the water column through wave action. As sea ice freezes, suspended sediments become incorporated into the ice, a process called suspension freezing (Wadhams 2000). This "dirty ice" can then be transported throughout the Arctic via the major current systems (e.g. the Transpolar Drift). Entrained sediment has been found to significantly reduce ice algal primary productivity and biomass (Gradinger et al. submitted), and is a likely cause of the relatively low biomass found in this study in the spring of 2004. Although sea ice chl *a* values were low relative to values during a typical spring bloom, chl *a* and POC concentrations in the ice were two orders of magnitude higher than concentrations in the underlying water column in May.

Stable isotope and gut contents show no evidence that *O. litoralis* had undergone a diet switch between March and May 2004, suggesting that there may not have been sufficient biomass in the ice to initiate a migration to the underside of the ice. Alternatively, it has been suggested that ice algae are not available to under-ice crustaceans until the ice begins to melt (Michel et al.1996). This is supported by observations made during the

pre-melting season in April 2003 (Gradinger and Bluhm 2005) when ice chl *a* was relatively high (71.4 ug/L), but *O. litoralis* guts contained low numbers of algal cells. After the onset of ice melt in late May, *O. litoralis* gut contents in that study revealed that ice algae had become their primary food source. This has also been documented in previous work looking at *O. litoralis* gut and fecal pellet contents (Carey and Boudrias 1987). In the present study, a diet shift to ice algae may have been detected in *O. litoralis* if sampling in 2004 had extended into the onset of ice melt.

4.7 Proportional contributions of food sources

Stable isotopes reflect a time averaged assimilation of a consumer's diet, and mixing models are useful tools for determining the proportional contribution of several sources to that diet (Phillips and Gregg 2003). The models are sensitive to the magnitude of the isotopic difference between the end members, to the diet-consumer fractionation factors chosen (Vander Zanden and Rasmussen 2001), and to the degree that the actual diet sources are represented in the model. In this study, *in situ O. litoralis* $\delta^{13}C$ and $\delta^{15}N$ ratios did not reveal that these amphipods were consuming any combination of the end members collected (POM_{ice}, POM_{water}, POM_{sed}). These results suggest that a) *O. litoralis* fractionation factors are very different than the fractionation factors used in the model and/or b) a major diet source of *O. litoralis* was not represented by any of the sources collected.

First, the generally accepted range of isotopic fractionation of 0-1‰ for $\delta^{13}C$ and 2-4‰ for $\delta^{15}N$ can vary greatly with species and taxa and have also been found to vary with the nutritive quality of a consumer's diet (Adams and Sterner 2000, Vander Zanden and Rasmussen 2001). However, during most sampling periods, for the three-source mixing model to work *O. litoralis* would have required fractionation factors far exceeding values that have been found in other crustaceans (McCutchen et al. 2003, Yokoyama et al. 2005).

Second, it is possible that a major diet source was not represented by any of the POM values collected over the year. *O. litoralis* lives a benthic lifestyle during times of low productivity in the ice or during ice-free conditions, feeding on meiofaunal crustaceans and scavenging dead or dying amphipods (Boudrias and Carey 1988). In this study, bulk POM from seafloor sediment was used to represent the benthic end member in the diet of *O. litoralis* during these times. In all sampling periods, bulk POM_{sed} $\delta^{15}N$ values were highly depleted, with all values near 0‰ $\delta^{15}N$. The large difference between $\delta^{15}N$ values of *O. litoralis* (13.6 to 15.4‰) and POM_{sed} (–0.3 to 1.6‰), particularly in December when there is no production in the ice or water column, suggests that these bulk sediment values are not representative of the benthic diet of *O. litoralis*. The coastline near Barrow and throughout much of the Arctic is prone to erosion during autumn storms (Lynch et al. 2004, Jorgenson and Brown 2005). The eroded land consists primarily of organic peat that is washed onto the beach, resulting in an influx of terrestrial material into the marine system. Peat tends to be depleted in both ^{13}C and ^{15}N (typical values of –28‰ and 0‰ respectively, Dunton et al. in press) compared to marine algae (Schell 1983, Kracht and Gleixner 2000). Although up to 50% of the organic material found in coastal Arctic seafloor sediments can be terrestrial in origin, peat carbon is thought not to be utilized by marine organisms and not to be incorporated into the marine food web (Schell 1983). Physically separating the marine organic matter (benthic diatoms, meiofaunal crustaceans, etc.) from the bulk sediment samples would likely have better represented the benthic end member and diet of *O. litoralis*.

Additionally, a major diet source may have been missed as a result of the inherent patchiness of ice algal biomass (Mundy et al. 2005). The variability in snow thickness overlying the ice, as well as the patchiness of entrained sediment within the ice can result in a highly patchy distribution of ice algal production (Mundy et al. 2005, Gradinger and Bluhm 2005). The May POM_{ice} samples were collected from an area of relatively low biomass, as evidenced by the observed sediment layer. If *O. litoralis* were actually feeding in a more productive and enriched patch of ice algae nearby, this diet source

would likely be represented in the stable isotopic composition of the amphipods, yet it would be missing from the mixing models used here.

At the time of the May sampling, ice chl *a* and POM values indicate the spring ice bloom had not yet reached its peak, and ice bottom temperature indicated that ice melt had not begun. These data suggest that there was little opportunity for amphipods to feed on ice algae at this time. This is supported by the lack of algal cells in the gut contents in May. Together, the data suggest that May sampling occurred too early to capture both ice algal enrichment and a diet switch from benthic to sea ice feeding in *O. litoralis*. Thus, timing is important for detecting seasonal dietary changes in ice-associated food webs. In future studies, ice bottom temperature or ice thickness measurements can be used in conjunction with ice algal abundance measurements to determine when this food source becomes available to under-ice grazers, including *O. litoralis*.

5. Conclusions

The utility of stable isotopes to estimate the contribution of ice-derived food to the diet of primary consumers is dependent on the difference in isotopic ratios of ice algae and phytoplankton at any given time. This study shows that ice algae are not inherently enriched relative to phytoplankton. Therefore, early in the season, ice feeding will be underestimated if the ice algal isotopic composition is too similar to that of phytoplankton. That said, it appears that ice algae may be largely unavailable to the under-ice community prior to the onset of melt. This limits the opportunity for feeding on ice algae early in the spring when they are isotopically indistinguishable from phytoplankton, reducing the degree to which ice material would be underestimated in a consumer's diet.

The results of the experimental study show that monitoring changes in stable isotope composition in *O. litoralis* can provide relatively recent dietary information, on the order of weeks to a month, and will likely be a useful indicator of *O. litoralis* feeding behavior in spring. Metabolic turnover rates found here are higher than what would have been predicted for a polar ectotherm based on previous work and assumptions about reduced physiological rates in polar species (Chapelle and Peck 1995, Peck 2002). These results highlight the risk of generalizing isotopic turnover in organisms based on physiology, taxa, and environmental temperatures, and stress the need for experimental investigations into stable isotope dynamics in species of interest to accurately interpret isotopic data from the field. Additionally, results found here suggest that fractional turnover rates may be highly variable over time, even within a single species. The wide range of half-lives found for *O. litoralis* in spring versus autumn suggests that the rate of isotopic change, even within a species may not be applicable at all times of the year. This is the first study that we are aware of to compare the rate of stable isotopic change in the same species during two seasons. Future studies on a broad range of taxa are necessary to determine the generality of these results.

Warming trends in polar regions and reductions in sea ice duration and extent (Parkinson et al. 1999, Stroeve et al. 2005) have focused attention on how these changes will affect high latitude marine food webs. This study is a first step toward using stable isotopes to determine the extent that sea ice production is transferred through sympagic crustaceans to higher trophic levels. Such knowledge will be useful in determining the effects a changing ice regime will have on higher trophic levels in the Arctic.

6. References cited

Adams, T. S. and R. W. Sterner, 2000. The effects of dietary nitrogen on trophic level ^{15}N enrichment. Limnol. Oceanogr. 45: 601-607.

Ambrose, W. G., C. von Quillfeldt, L. M. Clough, P. V. Tilney, and T. Tucker, 2005. The sub-ice algal community in the Chukchi Sea: large- and small-scale patterns of abundance based on images from a remotely operated vehicle. Polar Biol. 28: 784- 795.

Arar, E. J. and G. B. Collins, 1997. In vitro determination of chlorophyll a and phaeophytin a in marine and freshwater algae by fluorescence. US Environmental Protection Agency, method 445.0, revision 1.2.

Arndt, C. E. and F. Beuchel, 2006. Life history and population dynamics of the Arctic sympagic amphipods *Onisimus nanseni* Sars and *O. glacialis* Sars (Gammaridea: Lysianassidae). Polar Biol. 29: 239-248.

Attkinson, A., B. Meyer, D. Stübing, W. Hagen, K. Schmidt, and U. V. Bathmann, 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-II. Juveniles and adults. Mar. Ecol. Prog. Ser. 160: 63-76.

Auel, H., M. Harjes, R. de Rocha, D. Stübing, and W. Hagen, 2002. Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol. 25: 374-383.

Bluhm, B. A., D. Piepenburg, and K. von Juterzenka, 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol. 20: 325-334.

Bosley, K. L., D. A. Witting, R. C. Chambers, and S. C. Wainright, 2002. Estimating turnover rates of carbon and nitrogen in recently metamorphosed winter flounder *Pseudopleuronectes americanus* with stable isotopes. Mar. Ecol. Prog. Ser. 236: 233-240.

Boudrias, M. A. and A. G. Carey, Jr., 1988. Life history patterns of *Pseudolibrotus litoralis* (Crustacea: Amphipoda) on the inner continental shelf, SW Beaufort Sea. Mar. Ecol. Prog. Ser. 49: 249-257.

Bradstreet, S. W. and W. E. Cross, 1982. Trophic relationships at high ice edges. Arctic. 35: 1-12.

Brey, T., J. Pearse, L. Basch, J. McClintock, and M. Slattery, 1995. Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. Mar. Biol. 124: 279-292.

Carey, A. G., 1992. The ice fauna in the shallow southwestern Beaufort Sea, Arctic Ocean. J. Mar. Syst. 3: 225-236.

Carey, A. G. and M. A. Boudrias, 1987. Feeding ecology of *Pseudolibrotus* (= *Onisimus*) *litoralis* Kröyer (Crustacea: Amphipoda) on the Beaufort Sea inner continental shelf. Polar Biol. 8: 29-33.

Chapelle, G. and L. S. Peck, 1995. The influence of acclimation and substratum on the metabolism of the Antarctic amphipods *Waldeckia obesa* (Chevreux 1905) and *Bovallia gigantea* (Pfeffer 1888). Polar Biol. 15: 225-232.

Collie, J. S., 1985. Life history and production of three amphipod species on Georges Bank. Mar. Ecol. Prog. Ser. 22: 229-238.

Conde, D., S. Bonilla, L. Aubiot, R deLeón, and W. Pinos, 1999. Comparison of the areal amount of chlorophyll a of planktonic and attached microalgae in a shallow coastal lagoon. Hydrobiologia. 408-409: 285-291.

Cooper, L. W., J. M. Grebmeier, I. L. Larsen, V. G. Egorov, C. Theodorakis, and J. R. Lovvorn, 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Mar. Ecol. Prog. Ser. 226: 13-26.

DeNiro, M. J. and S. Epstein, 1981. Influence of the diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta. 45: 341-351.

Dower, K. M., M. I. Lucas, R. Phillips, G. Dieckmann, and D. H. Robinson, 1996. Phytoplankton biomass, P-I relationships and primary production in the Weddell

Sea, Antarctica, during the austral autumn. Polar Biol. 16: 41-52.

Dunton, K. H. and D. M. Schell, 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: $\delta^{13}C$ evidence. Mar. Biol. 93: 615-625.

Dunton, K. H., T. Weingartner, and E. C. Carmack, accepted. The nearshore Beaufort Sea ecosystem: Sources and fate of terrestrial carbon in Arctic coastal food webs. Prog. Oceanogr.

Frazer, T. K., 1996. Stable isotopes composition ($\delta^{13}C$ and $\delta^{15}N$) of larval krill, *Euphausia superba*, and two of its potential food sources in winter. J. Plankton Res. 18: 1413-1426.

Frazer, T. K., R. M. Ross, L. B. Quentin, and J. P. Montoya, 1997. Turnover of carbon and nitrogen during growth of larval krill, *Euphausia superba* Dana: a stable isotope approach. J. Exp. Mar. Biol. Ecol. 212: 259-257.

Frey, K., H. Eicken, D. K. Perovich, T. C. Grenfell, B. Light, L. H. Shapiro, and A. P. Stierle, 2001. Heat budget and decay of clean and sediment-laden sea ice off the northern coast of Alaska. Proc. Conf. Port Ocean Eng. Arctic Cond. 3: 1405-1412.

Fry, B. and C. Arnold, 1982. Rapid $^{13}C/^{12}C$ turnover during growth of brown shrimp (*Panaeus aztecus*). Oecologia. 54:200-204.

Gannes, L. Z., D. M. O'Brien, and C. M. Del Rio, 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology. 78: 1271-1276.

Garrison, D. L. and K. R. Buck, 1986. Organism losses during ice melting: A serious bias in sea ice community studies. Polar Biol. 6: 237-239.

Gibson, J. A. E, T. Trull, P. D. Nichols, R. E. Summons, and A. McMinn, 1999. Sedimentation of ^{13}C-rich organic matter from Antarctic sea-ice algae: a potential indicator of past sea ice extent. Geology. 27: 331-334.

Glazier, D. S., 1999. Is fatter fitter? Body storage and reproduction in ten populations of the freshwater amphipod *Gammarus minus*. Oecologia. 122: 335-345.

Gleitz, M., M. Rutgers v.d. Loeff, D. N. Thomas, G. S. Dieckman, and F. J. Millero, 1995. Comparison of summer and winter inorganic carbon, oxygen and nutrient concentrations in Antarctic sea ice brine. Mar. Chem. 51: 81-91.

Gorokhova, E. and S. Hansson, 1999. An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. Can. J. Fish. Aquat. Sci. 56: 2203-2210.

Gosselin, M., M. Levasseur, P. A. Wheeler, R. A. Horner, and B. Booth, 1997. New measurements of phytoplankton and ice production in the Arctic Ocean. Deep-Sea Res. II. 44: 1623-1644.

Gradinger, R. R., 2002. Sea ice microorganisms. In Bitten G. (Ed). Encyclopedia of Environmental Microbiology. Wiley and Sons, Hoboken, NJ. Pg. 2833-2844.

Gradinger, R. R. and B. A. Bluhm, 2004. *In-situ* observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. Polar Biol. 27: 595-603.

Gradinger, R. R. and B. A. Bluhm, 2005. Susceptibility of sea ice biota to disturbances in the shallow Beaufort Sea: Phase 1: Biological coupling of sea ice with the pelagic and benthic realms. Final report, OCS Study MMS 2005-062.

Gradinger, R. R., B. A. Bluhm, and M. R. Nielson, submitted. The pivotal role of sea ice sediments for the seasonal development of near-shore Arctic fast ice biota off Barrow, Alaska. Mar. Ecol. Prog. Ser.

Haddon, M., 2001. Modelling and Quantitative Methods in Fisheries. Chapman and Hall, Boca Raton, FL.

Herzka, S. Z. and G. J. Holt, 2000. Changes in isotopic composition of red drum (*Sciaenops ocellatus*) larvae in response to dietary shifts: potential applications to settlement studies. Can. J. Fish. Aquat. Sci. 57: 137-147.

Hesslein, R. H., K. A. Hallard, and P. Ramlal, 1993. Replacement of sulfur, carbon and nitrogen in tissue of the growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$. Can. J. Fish. Aquat. Sci. 50: 2071-2076.

Hobson, K. A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia. 120: 314-326.

Hobson, K. A. and R. G. Clark, 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor. 94: 181-188.

Hobson, K. A. and H. E. Welch, 1992. Determination of trophic relationships within a high Arctic marine food web using delta-13 C and delta-15 N analysis. Mar. Ecol. Prog. Ser. 84: 9-18.

Hobson, K. A., R. T. Alisauskas, and R. G. Clark, 1993. Stable isotope enrichment in avian tissues due to fasting and nutritional stress: Implications for isotopic analysis of diet. Condor. 95: 388-394.

Hobson, K. A., W. G. Ambrose, and P. E. Renaud, 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: In sights from delta C-13 and delta N-15 analysis. Mar. Ecol. Prog. Ser. 128: 1-10.

Hobson, K. A., A. Fisk, N. Karnovsky, M. Holst, J. Gagnon, and M. Fortier, 2002. A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Res. II. 49: 5131-5150.

Hochachka, P. and G. Somero, 2002. Biochemical Adaptation, Mechanism and Physical Evolution. Oxford University Press, New York.

Horner, R., S. F. Ackley, G. S. Dieckmann, B. Gulliksen, T. Hoshiai, L. Legendre, I. A. Melnikov, W. S. Reeburgh, M. Spindler, and C. W. Sullivan, 1992. Ecology of sea ice biota, 1: Habitat, terminology, and methodology. Polar Biol. 12: 417-427.

Horner, R., 1985. Sea Ice Biota. CRC Press, Boca Raton, FL.

Iken, K., B. A. Bluhm, and R. Gradinger, 2005. Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol. 28: 238-249.

Jardine, T. D., D. L. MacLatchy, W. L. Fairchild, R. A. Cunjak, and S. B. Brown, 2004. Rapid carbon turnover during growth of Atlantic Salmon (*Salmo salar*) smolts in sea water, and evidence for reduced food consumption by growth-stunts.

Hydrobiologia. 527: 63-73.

Johannessen, O., L. Bengtsson, M. W. Miles, S. I. Kuzmina, V. A. Semenov, G. V. Alekseev, A. P. Nagurnyi, V. F. Zakharov, L. P. Bobylev, L. H. Pettersson, K. Hasselmann, and H. P. Cattle, 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. Tellus. 56: 328-341.

Jorgenson, M. T. and J. Brown, 2005. Classification of the Alaskan Beaufort Sea coast and estimation of carbon and sediment inputs from coastal erosion. Geo-Mar. Lett. 25: 69-80.

Kempema, E. W., E. R. K. Reimnitz, and P. W. Barnes, 1989. Sea ice sediment entrainment and rafting in the Arctic. J. Sed. Petrol. 59: 308-317.

Kennedy, H., D. N. Thomas, G. Kattner, C. Haas, and G. S. Dieckmann, 2002. Pariculate organic matter in Antarctic summer sea ice: concentration and stable isotope composition. Mar. Ecol. Prog. Ser. 238: 1-13.

Kracht, O. and G. Gleixner, 2000. Isotope analysis of pyrolysis products from *Sphagnum* peat and dissolved organic matter from bog water. Org. Geochem. 31: 645-654.

Lavoie, D., K. Denman, and C. Michel, 2005. Modeling ice algal growth and decline in a seasonally ice-recovered region of the Arctic (Resolute Passage, Canadian Archipelago). J. Geophys. Res. 110: 1-17.

Lee, R. F., W. Hagen, and G. Kattner, 2006. Lipid storage in marine zooplankton. Mar. Ecol. Prog. Ser. 307: 273-306.

Legendre, L., S. F. Ackley, G. S. Dieckmann, B. Gulliksen, R. Horner, T. Hoshiai, I. A. Melnikov, W. S. Reeburgh, M. Spindler, and C. W. Sullivan, 1992. Ecology of sea ice biota 2. Global significance. Polar Biol. 12: 429-444.

Logan, J., H. Haas, L. Deegan, and E. Gaines, 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. Oecologia. 147: 391-395

Lønne, O. J and B. Gulliksen, 1991. Sympagic macro-fauna from multiyear sea-ice near Svalbard. Polar Biol. 11: 471-477.

Lønne, O. J. and G. W. Gabrielsen, 1992. Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. Polar Biol. 12: 685-692.

Lovvorn, J. R., L. W. Cooper, M. L. Brooks, and C. C. DeRuyck, J. K. Bump and J. M. Grebmeier, 2005. Organic matter pathways to zooplankton and benthos under pack ice In late winter and open water in late summer in the north-central Bering Sea. Mar. Ecol. Prog. Ser. 291: 135-150.

Lynch, A. H., J. A. Curry, R. D. Brunner, and J. A. Maslanik, 2004. Toward an integrated assessment of the impacts of extreme wind events on Barrow, Alaska. Bull. Am. Met. Soc. February: 209-221.

MacAvoy, S. E., S. A. Macko, and G. C. Garman, 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. Can. J. Fish Aquat. Sci. 58: 923-932.

MacAvoy, S. E., S. A. Macko, and L. S. Arneson, 2005. Growth versus metabolic tissue replacement in mouse tissue determined by stable carbon and nitrogen isotope analysis. Can. J. Zool. 83: 631-641.

Maruyama, Y. Yamada, B. Rusuwa, and M. Yuma, 2001. Change in stable nitrogen isotope ratio in the muscle tissue of a migratory goby, *Rhinogobius* sp., in a natural setting. Can. J. Fish. Aquat. Sci. 58: 2125-2128.

McCutchan, J. H., Jr., W. M. Lewis Jr., C. Kendall, and C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos. 102: 378-390.

McIntyre, P. B. and A. S. Flecker, 2006. Rapid turnover of tissue nitrogen in primary consumers in tropical freshwaters. Oecologia. 148: 12-21.

McMahon, K. W., W. G. Ambrose, B. J. Johnson, M. Sun, G. R. Lopez, L. M. Clough, and M. L. Carroll, 2006. Benthic community response to ice algae and phytoplankton in Ny Alesund, Svalbard. Mar. Ecol. Prog. Ser. 310: 1-14.

McWhinnie, M. A., 1964. Temperature responses and tissue respiration in Antarctic crustacean with particular reference to the krill, *Euphausia superba*. Antarct. Res. Ser. 1: 63-72.

Michel, C., L. Legendre, R. G. Ingram, M. Gosselin, and M. Levasseur, 1996. Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. J. Geophys. Res. 101: 18345-18360.

Mundy, C. J., D. G. Barber, and C. Michel, 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. J. Mar. Syst. 58: 107-120.

Parkinson, C. L., D. J. Cavalieri, P. Gloersen, H. J. Zwally, and J. C. Comiso, 1999. Arctic sea ice extents, areas, and trends, 1978-1996. J. Geophys. Res. 104: 20837-20856.

Peck, L., 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. Polar Biol. 25: 31-40.

Peinert, R., E. Bauerfeind, R. Gradinger, O. Haupt, M. Krumbholz, I. Peeken, I. Werner, and B. Zeitzschel, 2001. Biogenic particle sources and vertical flux patterns in the seasonally ice-covered Greenland Sea. In: Schäfer, P., Ritzrau, W., Schlüter, M., and Thiede, J. (eds). The Northern North Atlantic: A Changing Environment. Springer, Berlin, pp. 69-79.

Percy, J. A., 1993. Energy consumption and metabolism during starvation in the Arctic hyperiid amphipod *Themisto libellula*. Polar Biol. 13: 549-555.

Perga, M. E. and D. Gerdeaux, 2005. 'Are fish what they eat' all year round? Oecologia. 144: 598-606.

Peterson, B. J. and B. Fry, 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18: 293-320.

Phillips, D. L. and J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia. 136: 261-269.

Poltermann, M., 1998. Abundance, biomass and small-scale distribution of cryopelagic amphipods in the Franz Josef Land area (Arctic). Polar Biol. 20: 134-138.

Poltermann, M., 2001. Arctic sea ice as feeding ground for amphipods – food sources and strategies. Polar Biol. 24: 89-96.

Post, D. M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology. 83: 703-718.

Robertson, R. F., A. J. El-Haj, L. S. Peck, and E. W. Taylor, 2001. The effects of temperature on metabolic rate and protein synthesis following a meal in the isopod *Glyptonotus antarcticus* Eights (1852). Polar Biol. 24: 677-686.

Rothrock, D. A., Y. Yu, and G. A. Maykut, 1999. Thinning of the Arctic sea-ice cover. Geophys. Res. Let. 26: 3469-3172.

Runge, J. A. and R. G. Ingram, 1988. Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. Limnol. Oceanogr. 33: 280-286.

Sakano, H., E. Fujiwara, S. Nohara, and H. Ueda, 2005. Estimation of nitrogen stable isotope turnover rate of *Onchorynchus nerka*. Environ. Biol. Fishes. 72: 13-18.

Sakshaug, E., A. Bjørge, B. Gulliksen, H. Loeng, and F. Mehlum, 1994. Structure, biomass, distribution, and energetics of the pelagic ecosystem in the Barents Sea: A synopsis. Polar Biol. 14: 405-411.

Schell, D. M., 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: Delayed production from peat in Arctic food webs. Science. 219: 1068-1071.

Schmidt, K., A. Atkinson, D. Stübing, J. W. McClelland, J. P. Montoya, and M. Voss, 2003. Trophic relationships among Southern Ocean copepods and krill: Some uses and limitations of a stable isotope approach. Limnol. Oceanogr. 48: 277-289.

Schmidt-Nielsen, K., 1997. Animal Physiology: Adaptation and environment. Cambridge University Press.

Schnack-Schiel, S. B., 2003. The microbiology of sea ice. In: Thomas, D. N., Dieckmann, G. S. (eds) Sea ice: An Introduction To Its Physics, Chemistry, Biology And Geology. Blackwell, Oxford, pp. 211-239.

Schubert, C. J. and S. E. Calvert, 2001. Nitrogen and carbon isotopic composition of marine and terrestrial organic matter in Arctic Ocean sediments: implications for

nutrient utilization and organic matter composition. Deep-Sea Res. 48: 789-810.

Søreide, J. E., H. Hop, M. L. Carroll, S. Falk-Peterson, and E. N. Hegseth, 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog. Oceanogr. 71: 59-87.

Stroeve, J. C., M. C. Serreze, F. Fetterer, T. Arbetter, W. Meier, J. Maslanik, and K. Knowles, 2004. Tracking the Arctic's shrinking ice cover: Another extreme September minimum in 2004. Geophys. Res. Lett. 32: L04501, doi: 10.1029/2004GL021810.

Suzuki, K. W., A. Kasai, K. Nakayama, and M. Tanaka, 2004. Differential isotopic enrichment and half-life among tissues in Japanese temperate bass (*Lateolabrax japonicus*) juveniles: implications for analyzing migration. Can. J. Fish. Aquat. Sci. 62: 671-678.

Tamelander, T., P. E. Renaud, H. Hop, M. L. Carroll, W. G. Ambrose, and K. A. Hobson, 2006. Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea marginal ice zone, revealed by stable carbon and nitrogen isotope measurements. Mar. Ecol. Prog. Ser. 310: 33-46.

Thomas, D. N. and G. S. Dieckmann (eds), 2003. Sea Ice: An Introduction to Its Physics, Chemistry, Biology and Geology. Blackwell, Oxford.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade, 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia. 57: 32-37.

Tominaga, O., N. Ono, and T. Seikai, 2003. Influence of diet shift from formulated feed to live mysids on the carbon and nitrogen stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) in dorsal muscles of juvenile Japanese flounders, *Paralichthys olivaceus*. Aquaculture. 218: 265-276.

Tynan, C. and D. P. DeMaster, 1997. Observations and predictions of Arctic climate change: Potential effects on marine mammals. Arctic. 50: 308-322.

Vander Zanden, M. J. and J. B. Rasmussen, 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic

fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. 46: 2061-2066.

Wadhams, P., 2000. Ice In The Ocean. Gordon and Breach Science Publ., Amsterdam.

Werner, I., 1997. Grazing of Arctic under-ice amphipods on sea-ice algae. Mar. Ecol. Prog. Ser. 160: 93-99.

Werner, I., 2000. Faecal pellet production by Arctic under-ice amphipods – transfer of organic matter through the ice/water interface. Hydrobiologia. 426: 89-96.

Werner, I. and R. Gradinger, 2002. Under-ice amphipods in the Greenland Sea and Fram Strait (Arctic): environmental controls and seasonal patterns below the pack ice. Mar. Biol. 140: 317-326.

Werner, I and H. Auel, 2005. Seasonal variability in abundance, respiration and lipid composition of under ice amphipods. Mar. Ecol. Prog. Ser. 292: 251-262.

Witting, D. A., R. C. Chambers, K. L. Bosley, and S. C. Wainright, 2004. Experimental evaluation of ontogenetic diet transitions in summer flounder (*Paralichthys dentatus*), using stable isotopes as diet tracers. Can. J. Aquat. Sci. 61: 2069-2084.

Yokoyama, H., A. Tamaki, K. Harada, K. Shimoda, K. Koyama, and K. Ishihi, 2005. Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Mar. Ecol. Prog. Ser. 296: 115-128.

Appendix A

7.1 Experimental data - results

Table 7.1.1 Turnover experiment 1: Highly enriched treatment, 1°C. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 1, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	54.2	57.2	14.4	-22.2	7.8
1	55.7	65.5	12.8	-23.5	10.6
1	48.0	45.4	13.5	-21.4	8.8
1	34.4	40.1	12.8	-21.5	6.7
1	42.7	37.0	12.3	-21.1	7.2
7	29.9	29.3	11.7	-8.6	8.3
7	64.4	66.1	13.1	-16.4	8.9
7	65.7	63.4	13.1	-9.6	7.2
7	64.7	85.6	12.8	-11.2	7.0
7	42.8	41.3	11.9	-6.0	7.2
14	47.0	52.8	12.8	-11.5	7.4
14	75.0	101.1	12.7	-9.5	7.3
14	56.8	57.3	11.9	-3.9	7.7
14	54.7	63.6	11.4	-4.3	7.2
14	33.5	38.2	11.7	-10.3	6.4
21	47.7	47.7	11.9	-8.4	7.1
21	54.2	56.3	12.4	-6.2	7.0
21	71.4	93.1	11.8	-5.5	8.3
21	30.7	44.9	11.2	-2.6	6.8
21	46.1	42.7	11.5	-3.6	8.1
27	26.9	36.1	10.9	-2.3	7.8
27	61.7	59.0	11.8	0.0	6.8
27	70.4	95.6	12.2	-0.6	8.0
27	29.4	41.2	10.7	3.1	7.9
27	71.5	91.3	11.9	-6.3	7.1
35	51.8	75.3	10.9	1.3	7.9
35	26.1	34.3	12.0	6.0	5.6
35	43.3	48.3	11.4	10.8	6.7
35	65.0	84.9	11.2	0.0	7.0
35	52.9	62.5	11.9	-3.7	7.9
42	29.5	41.0	10.0	7.5	7.4

Table 7.1.1 continued

42	28.7	47.0	10.8	-2.6	6.6
42	64.1	79.1	11.1	0.8	7.4
42	65.5	89.5	11.3	4.8	6.4
42	60.3	84.2	11.1	1.0	6.9
49	59.7	80.4	10.9	13.0	7.5
49	60.1	82.4	10.9	9.2	7.4
49	50.3	64.8	11.3	-3.3	6.7
49	62.5	73.7	11.8	7.2	7.6
49	53.8	64.0	10.6	-0.6	6.7
56	60.3	80.2	11.0	8.5	6.5
56	55.7	72.5	11.3	8.9	5.8
56	44.3	63.2	11.8	4.7	5.6
56	28.4	61.8	10.3	12.8	5.8
56	67.6	97.5	10.4	1.9	7.3
63	54.0	78.2	10.5	12.6	5.5
63	54.2	78.2	10.2	10.7	6.0
63	52.8	69.6	10.4	7.1	5.8
63	55.7	78.1	10.4	9.1	6.6
63	66.3	83.9	11.2	0.2	7.2

Table 7.1.2 Turnover experiment 1: Highly enriched treatment, 4°C. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 1, maintained at 4°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	36.7	48.1	14.1	-21.6	6.5
1	47.8	48.4	13.5	-19.6	6.0
1	62.4	59.5	13.3	-19.4	6.9
1	40.0	43.7	12.4	-19.7	7.1
1	65.3	59.0	12.2	-23.0	7.7
7	59.2	81.7	14.1	-10.6	6.4
7	65.4	77.6	13.2	-8.9	6.3
7	71.5	65.7	12.0	-13.3	7.5
7	32.9	33.9	11.3	-3.0	6.7
7	72.0	88.5	12.4	-14.3	8.2

Table 7.1.2 continued

14	54.0	59.1	12.0	-15.9	8.3
14	60.3	77.1	11.5	-2.0	7.2
14	65.0	75.0	11.4	-1.7	6.4
14	51.5	68.0	13.5	-12.9	6.9
14	50.1	45.2	13.5	-12.9	8.4
21	53.1	49.9	11.0	3.6	7.5
21	71.2	83.1	11.6	-4.7	7.5
21	43.4	57.6	10.9	-4.0	6.8
21	71.5	85.4	11.6	-3.6	6.5
21	71.7	91.0	9.9	-1.2	7.8
27	67.4	82.8	12.0	10.1	5.6
27	70.4	73.5	14.3	-22.7	9.0
27	35.0	42.6	10.4	6.4	6.8
27	64.1	78.1	10.3	-2.5	7.1
27	39.7	54.4	10.7	7.4	6.4
35	54.8	72.7	11.0	8.6	5.8
35	54.6	80.8	10.2	6.0	7.0
35	53.6	73.7	10.8	-0.3	7.7
35	36.0	48.9	10.2	-3.0	7.3
35	42.7	57.0	11.1	5.1	7.1
42	74.6	91.6	11.8	-7.7	8.0
42	64.3	86.3	9.9	4.6	6.5
42	54.2	80.8	10.1	7.9	6.1
42	40.7	51.7	10.1	10.4	6.0
42	59.4	75.4	10.5	8.9	7.1
49	45.5	66.3	9.3	11.2	6.6
49	59.5	84.9	10.7	7.9	6.6
49	62.2	78.6	10.0	1.4	7.4
49	48.4	60.6	10.3	4.4	6.1
49	49.9	73.7	9.6	9.5	7.4
56	57.7	77.6	9.6	3.0	6.8
56	51.8	70.6	10.6	4.1	6.7
56	71.1	92.2	11.1	6.3	6.9
56	52.9	73.5	9.6	3.0	7.1
56	45.4	59.6	11.1	-5.2	7.7
63	53.1	77.2	9.7	8.0	7.0
63	29.8	50.7	9.7	18.4	6.7
63	55.3	81.5	9.6	6.7	6.8
63	35.6	72.4	9.6	9.5	7.1
63	53.4	70.5	10.0	8.7	7.1

Table 7.1.3 Turnover experiment 1: Moderately enriched treatment. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 2, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	54.8	67.9	13.8	-23.4	8.7
1	62.6	71.8	15.0	-21.5	5.6
1	55.6	53.4	14.0	-22.7	8.1
1	41.2	45.8	14.1	-21.0	7.6
1	46.6	39.9	13.7	-20.4	6.2
7	61.7	57.7	13.4	-18.9	5.6
7	33.1	43.9	12.5	-19.9	7.4
7	52.1	68.6	13.9	-21.1	6.5
7	48.0	48.8	12.1	-19.1	6.8
7	57.9	55.5	13.2	-18.3	5.9
14	56.9	59.1	12.8	-21.8	8.0
14	59.7	74.2	11.8	-20.3	7.6
14	47.2	51.6	13.4	-17.2	6.6
14	38.6	53.7	12.3	-19.4	7.6
14	47.3	61.2	13.6	-21.2	6.6
21	54.9	53.5	11.4	-19.5	6.8
21	54.9	77.9	12.0	-20.5	7.6
21	33.9	45.2	11.9	-18.4	6.5
21	63.7	61.6	11.5	-19.1	7.4
21	57.5	69.3	13.0	-20.2	6.8
27	50.5	74.5	11.9	-18.3	7.5
27	54.6	80.1	12.8	-20.5	7.4
27	68.8	90.2	13.4	-20.3	7.3
27	25.2	33.9	10.2	-17.4	7.0
27	48.1	56.7	11.5	-18.9	6.9
35	45.9	47.7	10.9	-19.3	7.5
35	74.6	94.4	12.5	-19.7	6.5
35	58.6	79.9	10.7	-16.9	7.3
35	48.9	70.6	10.7	-19.8	6.7
42	31.0	40.4	12.0	-17.6	6.4
42	58.5	84.4	11.6	-21.0	7.6
42	54.7	48.9	11.5	-19.9	6.7
42	62.9	80.4	10.8	-18.5	7.0
42	68.6	87.0	10.2	-18.0	6.0
49	54.0	67.7	11.8	-20.5	7.1
49	50.8	60.7	11.1	-18.9	6.7
49	53.7	68.2	11.3	-18.0	5.8
49	63.4	62.6	12.6	-18.6	6.4

Table 7.1.3 continued

49	48.6	66.2	10.7	-17.9	6.9
56	63.0	77.0	10.8	-18.5	6.0
56	68.9	92.8	10.2	-18.3	7.3
56	45.0	59.4	10.1	-16.2	6.5
56	64.3	65.9	10.1	-19.4	7.7
56	64.2	94.9	11.8	-20.4	7.9
63	59.3	83.6	11.9	-18.3	6.7
63	51.5	79.8	10.3	-18.4	6.2
63	58.4	77.5	10.6	-18.9	6.3
63	70.9	82.5	11.2	-17.9	6.3
63	66.5	86.3	10.7	-16.9	6.1
63	56.1	67.6	10.5	-18.1	7.9

Table 7.1.4 Turnover experiment 1: Fasting treatment. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving no food, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final δ15N	Final δ13C	C:N ratio
1	71.1	68.0	13.0	-19.3	6.0
1	61.2	69.3	12.7	-22.3	10.1
1	68.5	66.0	13.2	-22.2	9.6
1	60.8	61.0	13.9	-23.0	7.9
1	35.7	34.7	13.5	-21.8	8.9
7	45.3	46.8	13.7	-21.8	8.9
7	62.4	90.3	14.7	-22.9	7.6
7	66.0	81.0	14.0	-22.3	8.0
7	29.6	28.3	12.7	-21.3	8.2
7	54.0	48.8	13.7	-21.0	7.3
14	56.7	74.3	14.9	-21.2	5.4
14	58.3	75.6	14.1	-22.4	7.3
14	51.1	46.7	13.6	-22.0	7.3
14	30.9	32.0	14.1	-21.7	7.4
14	52.1	49.2	13.1	-21.2	7.7
21	27.9	35.3	13.9	-23.0	7.6
21	52.6	48.0	13.7	-20.8	6.3
21	46.4	42.7	14.4	-23.3	8.6
21	37.4	50.9	13.3	-22.7	7.6
21	69.5	82.9	14.1	-21.6	6.9

Table 7.1.4 continued

27	58.6	65.5	15.2	-21.6	6.8
27	66.9	86.2	14.8	-21.0	6.1
27	48.3	57.2	13.7	-22.8	10.1
27	56.3	52.6	14.1	-21.4	7.0
27	67.3	84.3	15.0	-21.4	6.2
35	63.0	61.5	13.7	-18.4	5.0
35	50.0	49.2	15.3	-21.9	7.4
35	66.1	78.2	14.2	-21.5	7.7
35	50.8	56.0	14.8	-20.0	5.2
35	45.8	42.5	14.4	-20.3	5.4
42	43.7	40.6	13.8	-23.0	5.1
42	67.4	84.1	14.5	-21.6	7.0
42	66.1	85.2	14.7	-23.3	8.0
42	61.1	83.0	14.3	-21.5	5.2
42	51.3	66.6	14.4	-22.7	6.5
49	53.3	66.1	15.2	-21.6	6.7
49	38.8	54.7	14.6	-22.1	5.0
49	62.5	84.4	14.8	-21.4	5.4
49	53.2	57.5	14.0	-22.4	5.6
49	62.3	54.3	13.4	-22.2	6.2
56	44.4	42.2	13.3	-22.5	7.8
56	61.0	61.1	15.1	-20.4	4.7
56	67.9	85.5	13.1	-21.7	6.1
56	60.0	64.8	16.1	-19.8	4.6
56	71.6	78.0	14.4	-21.6	6.3
63	54.7	53.2	14.3	-22.2	7.2
63	63.3	64.2	14.3	-22.4	7.1
63	45.1	44.8	15.0	-20.2	5.2
63	52.7	47.4	13.1	-20.2	5.3
63	59.1	59.5	13.6	-22.0	6.3

Table 7.1.5 Turnover experiment 1: Control treatment. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 3, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	27.5	23.2	11.6	-22.3	10.8
1	47.8	44.2	12.4	-22.7	9.6
1	46.8	46.2	13.5	-21.2	7.3
1	50.3	52.4	12.2	-20.8	8.4

Table 7.1.5 continued

1	57.2	51.9	13.0	-22.9	10.0
7	73.0	65.6	11.3	-21.8	7.9
7	60.2	86.1	12.6	-22.2	7.4
7	52.5	47.7	11.3	-22.3	8.1
7	64.0	59.3	10.2	-23.3	10.9
7	48.6	41.7	12.2	-22.4	8.3
14	37.1	55.4	11.2	-21.8	6.8
14	66.5	87.4	11.4	-23.1	7.5
14	53.6	65.8	11.4	-23.1	7.1
14	61.6	80.7	12.5	-23.4	10.5
14	61.4	80.9	10.9	-22.9	8.0

Table 7.1.6 Turnover experiment 2: Highly enriched treatment. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 1a, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	23.3	23.3	15.2	-18.1	6.3
1	77.1	77.1	16.1	-21.2	8.7
1	105.0	105.0	16.5	-20.0	6.0
1	109.5	109.5	16.2	-19.5	5.7
1	109.9	109.9	15.5	-18.8	6.5
5	54.0	54.0	15.7	-15.5	7.3
5	56.5	56.5	15.8	-15.0	7.5
5	57.3	57.3	15.7	-10.6	7.0
5	40.3	40.3	15.7	-14.7	7.1
5	71.6	71.6	15.5	-13.8	5.8
10	15.5	15.5	16.9	-2.1	7.4
10	30.6	29.6	16.5	-12.8	6.0
10	40.7	42.0	15.5	-18.8	7.5
10	59.0	58.5	15.1	-18.5	7.1
10	77.2	75.7	15.9	-19.2	6.9
15	25.3	25.6	16.2	-19.5	6.8
15	30.0	31.1	17.6	-0.5	7.4
15	42.2	42.0	16.5	-16.1	7.0
15	58.1	58.5	16.0	-12.4	6.5
15	59.9	58.2	16.3	-12.7	7.3
20	61.4	61.1	15.4	-19.3	6.9
20	67.4	64.3	17.1	-15.0	5.4

Table 7.1.6 continued

20	89.7	91.3	16.0	-12.4	6.7
20	96.7	96.6	15.5	-15.1	6.5
20	110.2	110.7	15.2	-16.1	6.8
27	22.8	29.9	19.2	-4.0	5.6
27	49.1	48.3	16.5	-18.1	8.3
27	62.8	62.8	16.6	-15.7	6.7
27	63.5	62.6	16.9	-17.9	5.9
27	80.3	78.6	17.2	-4.8	6.3
34	24.2	29.1	16.1	-15.7	6.7
34	26.7	26.7	17.9	30.9	7.0
34	41.1	41.6	17.1	-5.7	6.7
34	46.0	46.1	17.3	-6.5	6.1
34	80.6	81.0	16.7	-8.6	6.5
41	21.1	27.8	18.6	0.2	6.5
41	22.9	29.7	18.1	8.2	6.4
41	23.0	29.4	19.6	0.7	6.4
41	37.5	43.9	17.3	-15.8	6.6
41	42.5	42.8	17.3	-15.8	6.4
51	12.7	15.0	17.8	-1.3	6.3
51	71.5	78.1	16.7	-17.2	5.9
51	87.7	90.5	16.5	-12.7	5.1
51	96.2	97.9	16.8	-8.1	6.0
51	106.3	104.6	18.7	-12.8	7.0
61	24.4	31.8	17.2	-8.7	6.6
61	25.7	32.2	19.2	-8.5	8.2
61	59.8	65.2	19.0	-11.0	5.6
61	65.4	70.5	19.3	-6.4	6.4
61	68.1	72.3	17.4	-1.1	6.3
72	14.6	19.8	20.1	33.2	6.4
72	25.7	32.8	19.3	-1.0	6.3
72	38.8	43.9	19.5	4.3	6.8
72	42.5	51.2	19.4	3.7	6.7
72	50.4	64.5	19.7	-0.9	6.6

Table 7.1.7 Turnover experiment 2: Control treatment. Weights, $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of experimental amphipods receiving diet 3, maintained at 1°C.

Experimental Day	Initial weight (mg)	Final weight (mg)	Final d15N	Final d13C	C:N ratio
1	61.6	61.6	15.2	-20.4	7.2
1	37.9	36.9	16.2	-18.8	6.0
1	85.8	85.8	15.5	-21.0	9.3
1	55.0	55.0	15.5	-20.8	7.7
1	34.5	34.5	14.8	-19.4	6.9
5	63.8	63.8	15.9	-21.6	7.8
5	20.5	20.5	17.1	-19.7	7.4
5	53.4	53.4	15.8	-20.4	7.3
5	73.1	73.1	15.5	-21.0	6.6
5	57.1	57.1	14.7	-19.4	6.1
10	93.4	93.5	15.7	-19.9	6.6
10	23.6	23.6	16.5	-19.2	5.7
10	72.1	88.1	15.3	-20.2	7.1
10	66.7	68.4	14.8	-21.1	7.5
10	19.8	20.0	15.4	-20.8	6.7
15	30.8	29.2	15.1	-20.7	7.2
15	9.1	13.6	15.0	-20.1	6.1
15	45.8	43.9	14.0	-20.3	6.7
15	59.9	59.1	15.2	-19.2	6.9
15	37.5	37.0	15.5	-21.0	6.6
20	104.3	102.7	13.7	-20.4	6.7
20	95.8	96.3	14.4	-19.6	5.9
20	84.6	84.9	14.9	-19.6	5.5
20	29.3	29.5	15.2	-20.1	6.6
20	37.0	36.5	14.5	-20.6	6.3
27	85.2	83.4	13.8	-20.8	6.9
27	83.4	81.5	14.3	-20.7	6.2
27	34.2	34.9	13.3	-19.7	6.4
27	36.0	36.6	14.6	-19.8	6.1
27	56.6	57.1	13.6	-21.2	6.8
34	72.8	73.3	14.8	-19.2	5.8
34	52.7	59.5	14.0	-21.2	6.4
34	72.6	71.4	14.4	-19.7	6.7
34	72.1	72.0	14.4	-19.7	5.2
34	64.0	64.2	13.3	-21.1	6.7
41	41.5	41.5	14.2	-20.6	6.3
41	50.4	69.8	12.3	-21.5	7.8
41	65.0	65.7	14.0	-20.1	8.1
41	55.9	56.2	14.0	-20.6	6.5

Table 7.1.7 continued

41	81.9	84.1	13.3	-20.4	6.7
51	50.8	53.8	12.9	-20.8	6.5
51	27.8	29.3	13.0	-20.3	6.8
51	85.6	86.3	12.5	-20.0	8.2
51	31.1	39.4	11.9	-21.3	7.2
51	44.8	43.9	12.5	-20.0	6.0
61	67.3	75.6	12.1	-21.0	8.5
61	59.7	66.8	12.6	-19.5	7.8
61	75.3	77.2	13.4	-20.3	6.6
61	50.3	51.6	13.1	-20.0	7.1
61	69.6	68.1	13.6	-20.1	8.8
72	57.7	65.7	12.1	-21.2	8.2
72	52.5	59.2	12.5	-20.0	6.5
72	29.6	38.0	12.0	-20.2	7.0
72	51.2	55.4	12.8	-21.8	5.7
72	25.5	33.4	12.1	-20.8	6.7

Appendix B

7.2 Field data - results

Table 7.2.1 *Onisimus litoralis* field $\delta^{13}C$ and $\delta^{15}N$ values: $\delta^{13}C$ and $\delta^{15}N$ values and C:N ratios (by mass) of *O. litoralis* collected in March, May, September, and December 2004, near Barrow, Alaska.

Month	Replicate	d15N	d13C	C:N ratio
March	1	13.0	-21.4	9.2
	2	14.0	-20.2	6.3
	3	14.4	-20.8	6.5
	4	13.9	-22.1	8.0
	5	14.1	-22.3	7.6
	6	13.9	-21.8	7.5
	7	13.6	-22.8	8.3
	8	14.7	-21.1	6.4
	9	13.8	-21.1	6.9
	10	14.1	-22.3	7.8
May	1	13.3	-21.3	7.4
	2	14.6	-21.1	7.3
	3	13.9	-21.6	8.4
	4	13.4	-22.3	8.4
	5	14.4	-21.8	7.1
	6	14.3	-21.6	7.4
	7	13.4	-20.9	7.7
	8	13.2	-22.3	8.0
	9	13.5	-22.3	7.3
	10	14.8	-21.9	7.6
September	1	15.3	-18.7	5.5
	2	15.4	-19.5	5.8
	3	15.0	-19.5	5.5
	4	15.5	-20.2	7.3
	5	15.3	-20.2	6.5
	6	15.9	-19.5	6.9
	7	15.7	-18.7	5.5
	8	14.8	-20.1	6.8
	9	15.5	-20.0	5.7
	10	15.7	-19.9	6.0

Table 7.2.1 continued

December	1	12.8	-21.3	6.8
	2	13.3	-20.7	7.0
	3	13.7	-21.1	7.1
	4	14.7	-21.5	5.7
	5	14.0	-20.2	6.4
	6	13.7	-22.5	7.8
	7	13.9	-21.4	6.9
	8	12.3	-21.7	8.1
	9	13.3	-20.5	6.7
	10	13.9	-21.4	7.5

Table 7.2.2 $\delta^{13}C$ and $\delta^{15}N$ values, and C:N ratios (by mass) of particulate organic matter from sea ice, seawater, and seafloor sediment: samples collected in March, May, September, and December 2004, near Barrow, Alaska.

Month	sample	d15N	d13C	C:N ratio
March	ice	9.1	-24.2	13.9
March	ice	9.9	-24.1	13.3
March	ice	8.7	-23.5	11.3
March	ice	8.8	-23.6	11.5
March	water	11.4	-24.1	10.0
March	water	12.5	-23.8	9.6
March	water	11.3	-23.0	7.6
March	water	10.7	-23.5	8.5
March	Sediment	1.3	-23.0	8.1
March	Sediment	0.6	-23.8	7.3
March	Sediment	-0.7	-24.1	8.1
March	Sediment	0.3	-24.3	7.7
May	ice	9.1	-23.3	6.5
May	ice	9.2	-23.7	6.8
May	ice	9.1	-22.9	10.1
May	ice	10.9	-22.9	7.2
May	water	10.5	-21.7	7.9
May	water	9.9	-21.6	7.7

Table 7.2.2 continued

May	water	9.9	-22.3	8.4
May	water	11.9	-22.3	9.0
May	Sediment	3.9	-26.0	15.3
May	Sediment	0.7	-25.9	15.2
May	Sediment	2.2	-24.3	10.7
May	Sediment	-0.5	-24.3	8.4
August	water	17.6	-24.6	14.2
August	water	16.5	-24.2	13.2
August	water	16.2	-25.0	13.5
August	water	16.1	-25.9	12.1
August	Sediment	1.5	-24.2	8.2
August	Sediment	0.0	-25.6	10.3
August	Sediment	0.8	-24.5	8.1
August	Sediment	1.1	-24.1	7.7
December	water	14.3	-24.3	12.1
December	water	11.2	-24.6	7.8
December	water	14.7	-24.9	11.2
December	water	13.2	-24.7	11.4
December	ice	17.0	-24.1	12.3
December	ice	17.9	-24.0	13.9
December	ice	14.3	-23.7	11.4
December	ice	10.8	-24.4	14.5
December	Sediment	0.1	-25.7	13.9
December	Sediment	-0.1	-25.4	11.8
December	Sediment	-1.3	-26.0	14.2
December	Sediment	-0.1	-25.7	14.4